The influence of temperature on the geotropic presentation-time

by

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With Plate I.

INTRODUCTION.

§ 1. Recent views on the influence of tem-
perature on physiological processes.

The influence of temperature on physiological processes
has often been the subject of investigation. As early even
as the beginning of the nineteenth century determinations
were made of the maximum, optimum and minimum
temperatures of growth. It is especially since the resear-
ches of Sachs in 1860 that more and more importance
has been attached to these cardinal points of temperature;
and the curve representing the connection between a given
temperature and a physiological process (generally called
the optimum-curve) was thought fully to represent this
connection. In the second half of the nineteenth century
a good many investigators have tried in various cases to
determine this temperature curve, as it was thought the
end would be attained in a. given case, by the determina-
tion of the cardinal points of temperature.

This view has recently changed.

Not satisfied with the mere knowledge of the optimum-curve one has asked the cause of the inversionpoint in the curve and whether or no the occurrence and position of this inversion point are susceptible of further explanation.

In consequence the optimum-curve itself has been analysed. With regard to the actions of enzymes Duclaux in 1899 gave his opinion on theoretical grounds that the optimum-curve owes its origin to the summation of two curves. One of these curves would represent the continually increasing reaction-velocity, the other would show the even more rapid increase of the harmful influence of higher temperatures. In 1905 Blackman further developed this theory, added new ideas and adduced facts and figures in support of his argument.

As Blackman's line of thought has been taken as a guide for this investigation, it is necessary to give his considerations somewhat in detail. In the first place Blackman criticizes the conception of the optimum as a primary relation which holds good universally between temperature and a physiological process, and arrives at the conclusion that the optimum does not express a primary relation and must vary with the time of observation.

His starting-point is the rule that the reaction-velocity of certain chemical transformations increases two- to three-fold for every 10° C. rise of temperature. This law, known as van 't Hoff's law, holds good *in vitro* for all those reactions which take place slowly in aqueous solutions and resemble the reactions in the organism.

As early as 1901 Cohen pointed out in his „Vorträge für Aerzte über Physikalische Chemie," that this law may also be applied in biology; and he quoted some investigations from botany and zoology proving its validity.

Between 1905 and 1910 Kanitz published several papers on this subject and found that van 't Hoff's law was

applicable to the figures given by different investigators
for several physiological processes.

Blackman finds that van 't Hoff's law is valid in
the field of botany for temperatures roughly between
10° C. and 27° C., but above 27° C. quick falling off takes
place, so that at higher temperatures the values obtained
do not nearly reach those which might be expected if
calculated by van 't Hoff's law. Blackman, in his
explanation of this phenomenon, lays stress on a new
point of view, calling attention to the time-factor which
here comes into play. Sachs and Pfeffer had indeed
already pointed out the fact, that a short exposure to a
very high temperature is not so harmful as a prolonged
exposure to a slightly lower temperature, but up till then
very little attention had been bestowed upon the time-factor.

With the aid of Miss Matthaei's figures relating to
carbon-assimilation, Blackman traces the influence of
time and the deviations from van 't Hoff's law, which
this influence brings about.

He summarises his results in three laws:

1) At high temperatures (30° C. and above, for cherry-
   laurel) the initial rate of assimilation cannot be main-
   tained, but falls off regularly.
2) The higher the temperature the more rapid is the rate
   of falling off.
3) The falling off at any given temperature is faster at
   first and subsequently becomes less rapid.

The following diagram taken from Blackman's paper
represents graphically the figures found by Miss Mat-
thaei for the assimilation.

The dotted line gives the values calculated according
to van 't Hoff's law, starting from the values found
experimentally at lower temperatures. The other curves
are drawn through the ascertained values at higher tem-

peratures and continued beyond the actual estimations by extrapolation. At each temperature the assimilation-estimations were four in number, of one hour's duration each,
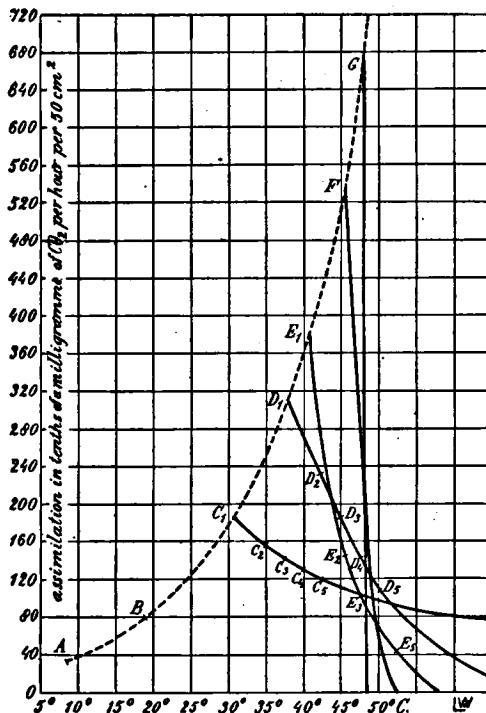

Fig. 1. Assimilation-curves, after Blackman.

preceded by one and a half hour's preliminary heating. In this way the assimilation was found for the first hour, the second hour, the third hour and the fourth hour. The values found at each temperature for the different hours of warming are all plotted in the same diagram; for this purpose the abscissae axis has been taken as time axis and for each temperature the ordinate of that temperature

as starting-point. At 30° C. e. g. the values C_2—C_5 found after 1—4 hours are plotted as beginning with the ordinate of 30° C. as starting-point, while afterwards the curve drawn through these points C_2—C_5. is continued backwards to C_1.

Now Blackman holds that the first experimentally found value for a given high temperature must already be too low; it is the value after one hour and we must have the value after a time zero. By extrapolation from the curve drawn through the points representing the values after one to four hours he gets the values for the time zero. This value must be identical with what he gets by calculating according to van 't Hoff's law. In the assimilation-diagram this indeed comes out fairly well, but the extrapolation from the time-curve may have been made somewhat arbitrarily.

Blackman comes to the conclusion that in many if not in all cases van 't Hoff's law would be found applicable to physiological processes and the optimum would vanish, if determinations could be carried out after warming during a time zero. At present the initial values are only to be found by extrapolation and calculation. The second part of Blackman's paper deals with „limiting factors."

When the rate of a process depends on a number of separate factors, the rate is limited by that of the slowest factor. This is virtually the same as „the law of the minimum", but its application to physiological reactions has mostly been overlooked.

Considering the case of assimilation we can recognise five factors which can control the reaction-velocity: the amount of CO_2 available, the intensity of available radiant energy, the amount of H_2O available, the amount of chlorophyl present and the temperature. If in investigating

the influence of one of these factors, e. g. the amount of
of CO_2 available, the amouut of radiant energy is insuffi-
cient, an increase of the amount of CO_2 will not be fol-
lowed by a proportional increase of the assimilation, for
the amount of available radiant energy does not allow a
further rise of assimilation. In that case the conclusion
is obvious, that assimilation is independent of the amount
of CO_2 available, but in reality the influence of the amount
of CO_2 available has not been observed, because the amount
of available radiant energy was acting as a limiting factor.

The following diagram 2, reproduced from Black-
man's paper, represents graphically the results to be
expected in such a case.
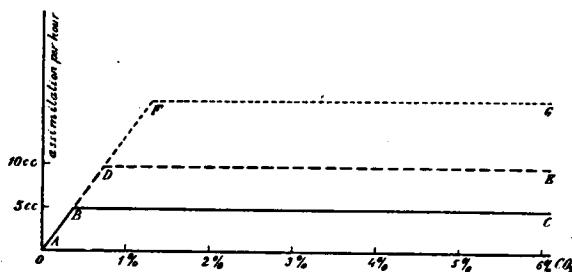
Fig. 2. Assimilation-curve, after B l a c k m a n.

The assimilation-curve A B, rising at first with the
amount of CO_2 available, becomes horizontal in B as soon
as the amount of available radiant energy does not allow
any further increase of assimilation. Had the amount of
radiant energy been greater, the curve would have gone
on rising to D and would have run horizontally from D
to E. These horizontal lines however do not give us any
idea of the relation between assimilation and the amount
of CO_2 available.

Since the publication of Blackman's paper several investigations have appeared, which have taken his theory into account. Thus in 1906 a paper was published by A. M. Smith, entitled: „On the application of the theory of limiting factors to measurements and observations of growth in Ceylon", in which Blackman's theory of limiting factors was subjected to practical tests.

Smith has found, that with the main axis of the inflorescence of *Agave* and *Furcraea* the temperature always limits the rate of growth. In this case therefore the temperature was continually the limiting factor. With *Dendrocalamus* — which he investigated at three different places in Ceylon having different climates — temperature and water-supply alternately came into play as limiting factors of growth; the water-supply itself was dependent on the humidity of the air and the light.

In summarising Smith thinks the theory of limiting factors a fruitful means for the explanation of many different phenomena of growth, and in one case only he does not succeed in reconciling all facts with this theory.

The further investigations founded upon the ideas of Blackman deal primarily with van 't Hoff's law and the variability of the optimum.

In 1907 Smith published a communication of a few lines on the respiration of *Hydrilla verticillata*. The intensity of respiration rises here from 7° C. — 50° C. according to van 't Hoff's law with a coefficient 2.2 for every rise of 10° C. An optimum with a subsequent decrease is absent here.

In 1908 Lawrence Balls published figures on the growth of fungus hyphae from which he concluded that between 15° C. and 30° C. the growth in this case followed van 't Hoff's law. Because these experiments were carried out by a method not wholly free from objections,

no further reference will be made to this subject (cf.
Kuyper, 1910, p. 136).

In the same year 1908 yet another communication
appeared, by Blackman himself, namely his opening-
address to the botanical section of the British Association.

In this address, which begins and ends with an attack
on the physiology of stimulus, Blackman explains how
physiology has to take cognisance of the principles of
physical chemistry and to apply them in solving its problems.

Further he gives a short explanation of the principles of
physical chemistry of which a botanist has to take ac-
count, and mentions the following:

1) the reaction-velocity, whereby he remarks that every
reaction is characterised by its own specific reaction-velocity;

2) the law of mass, which says that the reaction-
velocity is proportional to the concentration of the sub-
stances participating in the reaction;

3) the influence of catalytic agents, which have a pre-
ponderating influence in the organism;

4) the increase of the reaction-velocity with temperature,
which is so universal, that it must be present in the
living organism too.

Metabolism in plants is consequently discussed from
this point of view as a catalytic reaction and Blackman
traces how far the facts support the conclusion that the
four above mentioned principles are fundamental in this
case also. Summarising the writer says: „Three sets of
phenomena we have observed which, though usually treated
in the category of stimulation, draw a clearer interpretation
from the conception of reaction-velocity. These are: 1) the
relation of development to the absence or deficit of single
essential food constituents; 2) the occasional striking effect
of minute traces of added foreign substances upon the
whole rate of growth and metabolism; and 3) the general

doubling of the activity of vital processes by a rise of 10° C."

Although the author is evidently convinced that his theory will have to apply over the whole field of plant physiology, there are nevertheless processes to which he has not yet been able to extend his conclusions, at least he says at the end of his second paper. „Finally, superposed upon all this comes the first category of phenomena that we are content still to regard as stimulatory. — From our present point of view vision does not extend to the misty conceptions of stimulation upon our horizon."

In this investigation an attempt will be made to apply the ideas developed by Blackman to the field of pure physiology of stimulus and to test their general validity by the facts.

The next publication, in which the author shares Blackman's views, was a paper by J. Kuyper, which appeared in 1909, and dealt with the influence of temperature on respiration. [1]

According to the conclusions of this investigation the conception of Blackman is partly applicable to respiration.

Up to 10° C. the same quantity of CO_2 is expired in successive hours and from 10° C. to 20° C. there is a slight increase during successive hours, then follows a period in which the production of CO_2 oscillates, while above 40° C. a regular decrease takes place which represented graphically gives an almost logarithmic curve. Van 't Hoff's law holds good for *Pisum* and *Triticum* from 0° C.—20° C. for *Lupinus* up to 25° C.; the coefficient for a rise of temperature of 10° C. lies between 2 and 3.

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1) As Dissertation, Utrecht, 1909; in 1910 published in Recueil des Trav. Botan. Néerl., Vol. 7, 1910. The quotations are taken from this last publication.

The optimum varies with the time of observation. Extra-
polation of the time-curves in order to obtain the values
after o time, did not give the values which should be
obtained if B l a c k m a n's theory applied fully. Finally
mention must be made of a publication which appeared
in 1910, by V a n I t e r s o n and Miss v a n A m s t e l,
wherein the considerations of B l a c k m a n are submitted
to a renewed investigation. The question was put, whether
or not the dependence on temperature of alcoholic fermen-
tation and of the action of invertase on cane-sugar was
in agreement with v a n 't H o f f's law. The writers conclude,
that v a n 't H o f f's law does not apply to this case and
hence their first conclusion runs: „it should thus be
pointed out very emphatically that even on account of
the course of the optimum-curve below harmful tempera-
tures the theory of D u c l a u x and B l a c k m a n must
be rejected.“   .

In this investigation the reaction-velocity after a warming-
time of 0 minutes was determined on different lines and
the result obtained by the authors is „that the curve
which refers to a preliminary warming-time of 0 minutes
is a pronounced optimum-curve, as well in the case of
alcoholic fermentation as in that of the inversion of
sugar.“ — „The opposite results at which B l a c k m a n
arrived and with reserve K u y p e r too, are in our opinion
due to the fact, that the velocity of the physiological
reactions measured by these investigators, was small
compared to the velocity with which the subsidence
took place.“

In Chapter III, when discussing my own results, I will
again return to these investigations, especially to the
last mentioned.

§ 2. Preliminary investigations on the influence of temperature on geotropism.

The influence of temperature on geotropic phenomena has been traced chiefly by Czapek and by Bach, whose results however do not agree in all points.

The earliest experiments of Czapek were published in 1895. With the purpose of investigating, whether perception and reaction could be separated, roots of *Vicia Faba* and *Lupinus* and hypocotyls of *Helianthus* were stimulated at 0° C., at which temperature growth and therefore reaction is impossible.

Perception appeared to be possible at 0° C.; the presentation-time at 0° C. amounted to about 18 hours according to these experiments. In addition, comparative experiments were made to determine the time during which a stimulation subsides at ordinary temperature and at 0° C. In the last case the subsidence is much faster.

A few years later Czapek traced the influence of temperature more fully; the figures obtained in this research are to be found in his paper of the year 1898.

The following table gives a summary of the results, obtained with germinating roots of *Lupinus albus*.

Lupinus albus, germinating roots.

Temperature.	Presentation-time.	Reaction-time.
0°	18 hours.	∞
5°	45 min.	360 min.
10°	30 „	120 „
15°	20 „	80 „
20°	20 „	80 „
25°	20 „	80 „
30°	20 „	70 „
39°	25 „	120 „

Thus Czapek found that the presentation-time and the reaction-time change at low and at high temperatures, but at temperatures between 15° C. and 30° C. they appear to be independent of temperature.

In 1907 Bach made a similar series of determinations for seedlings of *Vicia Faba* and found a much greater dependence on temperature, as is shown by the following table:

Vicia Faba, seedlings.

Temperature.	Presentation-time.	Reaction-time.
14°	14 min.	122.8 min.
17°	11 „	115.4 „
20°	7½ „	97.9 „
25°	3 „	64.8 „
30°	2 „	48.2 „
35°	4 „	80.8 „

The concluisions, drawn by Bach from this table are the following:

1) With regard to their length the presentation-time as well as the reaction-time show a very marked, regular dependence on temperature between 14° C. and 35° C.

2) This dependence is of the same kind for presentation-time and reaction-time; from 14° C. upwards there is a decrease with a minimum at 30° C. and afterwards again a rise in presentation-time and reaction-time. –

Bach was not able to explain the difference between his results and those of Czapek.

Besides these investigations, extending over a series of temperatures, papers are to be found here and there in the literature, dealing with the influence of a definite temperature on geotropic phenomena.

Thus H a b e r l a n d t published in 1902 and in 1903 experiments in support of the statolith-theory; he used plants which were grown out of doors during winter and afterwards transferred to a temperature of about 20° C. These experiments led H a b e r l a n d t to the conclusion that negatively geotropic stems, freed from starch by a prolonged sojourn at a temperature of a few degrees above 0° C., are not able to curve geotropically before the starch is regenerated.

Similar experiments were made in the same year by F r a n c i s D a r w i n, with much the same results. D a r w i n kept his objects of experiment from 6 to 26 hours at 33° C.—38° C. and by means of these high temperatures he too was able to eliminate starch more or less completely. Here also this elimination was accompanied by a more or less complete disappearance of the faculty for geotropic reaction.

Control-experiments, in which the phototropic reaction of plants thus treated was investigated, showed that the faculty for phototropic reaction decreased at nearly the same rate, so that Darwin did not regard these experiments as proving the validity of the statolith-theory.

Evidently of quite a different nature are the cases, principally investigated by V ö c h t i n g (1898) and L i d f o r s s (1903), for which V ö c h t i n g has proposed the name psychroclinic reactions. Both investigators found that a change of temperature causes a change of disposition with regard to geotropism, especially in spring-plants.

Several plants, diageotropic at low temperature, become negatively geotropic when the temperature rises, while conversely they change again from negative geotropism to dia-geotropism when the temperature falls.

As these phenomena are insufficiently known and do not bear directly on the present investigation, I have not

dealt further with them and have only alluded to them for the sake of completeness.

Lastly it should be mentioned here, that M a i l l e f e r, in his paper on geotropism which appeared in 1909 and also dealt with the influence of temperature, deduced a formula for this influence from B a c h's figures.

Maillefer himself however remarks, that the figures on which his formula is based were insufficient and that this formula can only be used with great reserve.

In Chapter III, in discussing my own results, the conclusions of these various writers will be subjected to criticism.

§ 3. Object of the present investigation.

When comparing what was said in § 1 about recent views concerning the influence of temperature on physiological processes with our review of the publications dealing with the relation between temperature and geotropism, as given in the previous section, it is clear that up till now these ideas have not been applied to the field of physiology of stimulus.

It is the purpose of this investigation to study the influence of temperature on the process of geotropic stimulation from Blackman's point of view with the object of ascertaining whether the ideas developed by him are applicable to this case. Here I will briefly indicate, by what means I have tried to attain this end.

As measure for the influence of temperature the presentation-time was chosen, because this quantity is theoretically and experimentally the best known in the process of geotropic stimulation and is moreover suitable for an exact quantitative investigation.

The reaction-time is only dealt with in so far as the accounts of the experiments relating to the presentation-

time also give the figures referring to the reactiontime. The time factor as Blackman called it was introduced by warming the objects of experiment (coleoptiles of *Avena*) one or more hours before the induction.

Besides investigating generally the influence of temperatures between 0° C. and 40° C. on the geotropic process, as judged by the changes in the presentation-time, I have especially sought an answer to the three following questions: 1) the validity of van 't Hoff's law; 2) the variability of the optimum in relation to the time factor; 3) the occurrence of limiting factors.

For a further statement of the reasons which led to the adoption of this method the reader is referred to § 4—§ 7, where everything is discussed in detail.

CHAPTER I.

METHOD.

§ 4. Detailed description of the method.

At the beginning of the experiment the experimental plants were placed in the thermostat (of § 6) at the temperature, the influence of which was to be traced, and they were stimulated after they had been in the thermostat for one or more hours. After the stimulation they were brought back to ordinary temperature (18° C.—21° C.), when the reaction was awaited and was examined by red light at intervals of 5 minutes.

The plants were not put on the clinostat during the latent period (between the stimulation and the moment when the reaction becomes visible), since Mrs. Rutten— Pekelharing [1]) has shown — and I have found this to

1) Rutten—Pekelharing, 1910, p. 258 and 259.

be true in several preliminary experiments — that the
same result is obtained, when the stimulated plants are
placed vertically in the ordinary way.

One hour's preliminary warming was taken as a mini-
mum, as on account of the construction of the thermostat,
the vessel with mould only acquired a constant tempera-
ture after that time.

At the same time it was verified by several thermo-
electrical determinations, that this time of preliminary
warming was necessary and sufficient.

Nevertheless the presentation-time was also determined
after a longer period of preliminary warming with the
twofold object of ascertaining whether the influence of
the temperature made itself felt after a longer time only,
and of thus being able to take into account the time-
factor according to Blackman. The columns for 1
hours', 2 hours', 4 hours' etc. preliminary warming in the
following tables, are therefore not strictly accurate, be-
cause the 1st hour is not strictly comparable to the
subsequent ones, since the time needed to arrive at
a given temperature is included in the first hour. That
time is of course shorter for the coleoptiles than for the
mould, but still it takes up a considerable part of the first
hour (cf. § 7).

The first determination was always of the presentation-
time after a stay of one hour at the temperature in ques-
tion. There upon a determination followed after 4 hours'
(or sometimes 6 or 8 hours') preliminary warming. If
no alteration of the presentation-time showed itself (as
was the case from 0° C.—25° C.), no further determinations
at that temperature were made; if any alteration was
seen, an endeavour was made to represent this alteration
as fully as possible and determinations were made after

preliminary warming for 1, 2, 4, 6, 12 and 24 hours and sometimes also even after 8, 18 and 48 hours.

The temperatures, at which determinations were made, lay between 0° C. and 40° C., with intervals of 5° C. Between 35° C. and 40° C. experiments were further made at 37° C., 38° C. and 39° C., because the presentation-time here increases extraordinarily fast. At 40° C. the presentation-time had already risen to 260 minutes after only one hours' stay in the thermostat and therefore no determinations were carried out at higher temperatures. Nor was the presentation-time determined below 0° C., as the results expected would not have been worth the trouble.

All the experiments took place in the dark room (cf. § 6) of the Botanical Laboratory at Utrecht, in an electrical thermostat, constructed specially for this purpose, so that the experiments were uniform with regard to this point. The plants were always stimulated by means of gravity at an angle of 90° by placing the vessels with plants (cf. § 5) vertically with the aid of the axis in the thermostat. In order to determine the presentation-time in a given case, I proceeded as follows. A set of plants were stimulated during a time, which I supposed to be nearly equal to the presentation-time. Then I concluded from the percentage of curved plants, whether the stimulation must be lengthened or shortened to reach the presentation-time. The series of determinations was then increased, if possible, until it extended from a stimulation-time with 0 % curved plants to one with 100 %. From this series the presentation-time itself (50 % curved) could be determined very accurately.

At first I took a large number of plants in each experiment, mostly 50 or 100 at each determination, hoping in this way to be independent of the individual variability (cf. § 7). Later I had to restrict myself because of the

enormous extension of the investigation, and on an average 25 plants were taken for each experiment.

Every experiment has its serial letter and a number, while the observations during the experiment were noted down by filling in forms previously hectographed.

Series A, experiments 1—222, extending from October 20th to December 31st 1909, includes preliminary experiments only on the material and the influence of external conditions, temperature excepted. Paragraphs 6 and 8 are chiefly concerned with these experiments.

Series B, experiments 1—81, extending from January 1st to February 19th 1910, also includes preliminary experiments, chiefly on the purity of the atmosphere and the influence of the thermostat. Only the first determination of the presentation-time at 0° C., after one hours' preliminary warming, and a few figures at 30° C., after one hours' preliminary warming, are also used later on.

All other experiments mentioned here belong to series C, experiments 1—374, extending from Febrnary 24th to August 12th 1910.

In order to give a true idea of the method employed by me I here describe one determination of the presentation-time in detail, the determination of the presentation-time after remaining 4 hours at 30° C. I therefore reprint here the protocols of the experiment with all details they contain.

<div align="center">C. Experiment 25. Date 11—III—1910.</div>

Stimulation-time: 3′30″. Temp.: 30° C. % 100.
Vessel: 4, 5, 6. Age: 4 days. Length: 10—25 mm.
Temp. of room: 21° C. Humidity: 75°.
In thermostat: at 4. Preliminary warming: 240′.
Horizontal: 8—8.3′.30″.

Number: 60   Curved after:

30 minutes: 12	35 minutes: 30	40 minutes: 47
45 „ : 50	50 „ : 56	55 „ : 58
60 „ : 60	65 „ : —	70 „ : —
75 „ : —	80 „ : —	85 „ : —

C. Experiment 30. Date: 14—III—1910.

Stimulation-time: 3′.   Temp.: 30° C.   % 82.
Vessel: 3, 4.   Age: 4 days.   Length: 10—25 mm.
Temp. room: 18° C.   Humidity: 60°.
In thermostat: at 10.15.   Preliminary warming: 250′.
Horizontal: 2.25—2.28.

Number: 50.   Curved after:

30 minutes: 0	35 minutes: 9	40 minutes: 17
45 „ : 26	50 „ : 32	55 „ : 36
60 „ : 40	65 „ : 41	70 „ : 37
75 „ : —	80 „ : —	85 „ : —
90 „ : 15.		

C. Experiment 33. Date: 16—III—1910.

Stimulation-time: 2′30″.   Temp. 30° C.   % 74.
Vessel: 3, 4.   Age: 4 days.   Length: 10—25 mm.
Temp. of room: 18° C.   Humidity: 70°.
In thermostat: at 9.50.   Preliminary warning: 240′.
Horizontal: 1.50—1.52.30.

Number: 50.   Curved after:

30 minutes: —	35 minutes: 5 ?	40 minutes: 12
45 „ : 24	50 „ : 30	55 „ : 33
60 „ : 37	65 „ : —	70 „ : 32
75 „ : —	80 „ : —	85 „ : 14

C. Experiment 41. Date: 19—III—1910.

Stimulation-time: 2′.   Temp.: 30°.   % 44.
Vessel: 5, 6.   Age: 4 days.   Length: 10—25 mm.
Temp. of room: 17° C.   Humidity: 70°.

In thermostat: at 10.   Preliminary warming: 245'.
Horizontal: 2.5—2.7.
Number: 50.   Curved after:

30 minutes: 4?	35 minutes: —	40 minutes: 17
45 „ : 17	50 „ : 20	55 „ : 22
60 „ : 20	65 „ : —	70 „ : 20
75 „ : —	80 „ : —	85 „ : —

C. Experiment 45. Date: 21—III—1910.

Stimulation-time: 1'30".   Temp.: 30° C.   % 30.
Vessel: 5, 6..   Age: 4 days.   Length: 20—30 mm.
Temp. of room: 17° C.   Humidity: 70°.
In thermostat: at 10.35.   Preliminary warming: 240'.
Horizontal: 2.35—2.36.30.
Number: 40.   Curved after:

30 minutes : —	35 minutes : 4?	40 minutes : —
45 „ : 6	50 „ : 11	55 „ : 12
60 „ : 12	65 „ : 12	70 „ : —
75 „ : 10	80 „ : —	85 „ : —

C. Experiment 46. Date: 21—III—1910.

Stimulation-time: 1'.   Temp. 30° C.   % 0.
Vessel: 7, 8.   Age 4 days.   Length: 10—25 mm.
Temp. of room: 17° C.   Humidity: 70°.
In thermostat: at 10.35.   Preliminary warming: 250'.
Horizontal: 2.44—2.45.
Number: 45.   Curved after:

30 minutes: 0	35 minutes : —	40 minutes : 0
45 „ : 0	50 „ : 0	55 „ : 0
60 „ : 0	65 „ : —	70 „ : —
75 „ : —	80 „ : —	85 „ : —

Summarising the results of these six experiments in
the same way as all the figures are tabulated at the end
of the second chapter, we get:

30° centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	DATE.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent of curved plants.
3′30″	C 25	11-III-1910	60	60	—	—	100
3′	C 30	14-III-1910	50	41	—	—	82
2′30″	C 33	16-III-1910	50	37	—	—	74
2′	C 41	19-III-1910	50	22	—	—	44
1′30″	C 45	21 III-1910	40	12	—	—	30
1′	C 46	21-III-1910	45	0	—	—	0

The presentation-time after 4 hours' preliminary warming at 30° C. is thus (rounded off to 10″): 2′10″.

This case is a very simple one, as none of the determinations had to be repeated, because they were in harmony with each other from the beginning: with a shortening of the stimulation-time the percentage of curved plants decreased regularly. Mostly this was not the case after one determination and some or even all determinations had to be repeated one or more times, till the average values showed a regular decrease with decreasing stimulation-time. Hence the columns „total number of plants used" and „total number of plants curved" have been added to all tables.

§ 5. Experimental object.

In all my experiments coleoptiles of *Avena sativa* only served as experimental objects. In my selection I was guided by the conviction, that it was most important to

find an object suited to exact quantitative working; the same motive has restrained me from extending my investigation to other plants. Besides, an exhaustive study of one object is worth more than a superficial investigation of many plants, and the time available was not sufficient for an exhaustive investigation of more than one object.

All seedlings used were from the same lot of oats, bought at W. C. Verbeek's in Utrecht in October 1909. Probably it would have been better had I used a pure strain, but this only occurred to me after I had already started my experiments, and so it was too late to adopt this precaution. The coleoptiles of *Avena* are especially well fitted for geotropic investigations, as has been remarked again and again. The simple shape of the coleoptile makes it possible to observe the first beginning of the reaction very accurately. For all anatomical particulars I refer to Rothert[1]; Blaauw[2] gave a description of the method of growing the seedlings, which I have followed with but few alterations.

As I did not invariably succeed quite well in growing a quantity of seedlings sufficient for my experiments, I wish to describe in detail the method, which yielded the best results. For further particulars concerning the object of experiment I refer to § 7, where all peculiarities of the Avena-coleoptiles will be mentioned again in discussing the sources of error.

The husked oat-grains were soaked by Blaauw[3] in water in earthen ware dishes, by Mrs. Rutten-Pekelharing[4] on moist saw-dust. I was much more satisfied with the method, used by Pringsheim[5], of soaking

1) W. Rothert, 1894.
2) A. H. Blaauw, 1909.
3) A. H. Blaauw, 1909, p. 11.
4) C. J. Rutten-Pekelharing, 1910, p. 254.
5) E. Pringsheim Jr., 1909.

the grains by spreading them on wet filterpaper. The
germination then takes place much more regularly. In
order to keep the filterpaper wet, it was laid on a flat
glass dish, turned upside down in the earthen ware dish.
The latter was filled with water so that the filterpaper
was always in contact with the water. The earthen ware
dish was covered with a second one.

After two days, germination had proceeded far enough
and uniformly enough, so that I could plant about 50 %
of the grains. This was done in the same vessels of zinc,
measuring 20 × 3 × 3 cm., that had been used by
Blaauw and also by Mrs. Rutten-Pekelharing. In
most cases I planted not one, but two rows in every
vessel so that each vessel contained 30 to 36 plants.
After two days in the dark in wooden boxes of 50 × 30 ×
20 cm, doubly lined with dark cloth and covered in the
same way, the coleoptiles had reached a sufficient length
(10 to 35 mm) to be used in the experiments. Specimens
that were not quite straight or plants of which the hypo-
cotyl had developed, had been previously removed and
for convenience sake the number was often reduced to
25 in each vessel. In addition the vessels were watered
by means of a small spray on the morning of the second day.

The greatest difficulty encountered in growing the
seedlings was the growing out of the hypocotyl. In the
beginning this scarcely ever happened, later on (after
about March 1910) it gave me much trouble. Again and
again I had to destroy whole batches for this cause. When
the hypocotyl grows out, it grows in the direction it has
underground without altering this direction as it is not
geotropically sensitive. Consequently it mostly protrudes
obliquely from the soil and so the coleoptile also slants.
The latter afterwards bends itself geotropically and so
it is of no use for the experiment.

Blaauw also mentions this difficulty of the hypocotyls
growing out and he too was especially troubled by it in
spring, as he has told me himself. He thinks [1] that low
temperatures during the growing have an unfavourable
influence, but I cannot share his view on the ground of
my own results. I am rather inclined to think, that high
temperatures facilitate the growth of the hypocotyls,
although straight plants are also obtainable at high
temperatures, as appeared in experiments, in which the
objects of experiment were kept at 35° C. during 24 hours.
The main cause, as it seems to me, is to be sought in
the want of fresh air, although I cannot adduce conclusive
experiments in support of this opinion. The method of
growing in doubly covered wooden boxes does not improve
the ventilation; moreover the atmosphere of the laboratory
is generally injurious (cf. § 7). Obviously it would have
been best to put the boxes, in which the oat-seedlings were
grown, out of doors in the fresh air, if a constant or nearly
constant temperature were not also necessary for growing.
In the beginning all the objects were grown in the hothouse of
the institute, as this stands quite apart from the laboratory,
is lighted with electricity and is steam-heated. There I
was only troubled by the growing out of the hypocotyls,
when the temperature rose on sunny days and sometimes
at week-ends, as on Sundays the boxes were not aired.
After the 9th of March I had to leave the hothouse as it
was impossible to keep its temperature low enough on
sunny days. The only room I could use for further growing
was the dark room, where I also made my experiments.
This room, situated quite within the building remained
pretty well at the same temperature and an electric fan
enabled me to ventilate it the whole day at will. Never-

1) A. H. Blaauw, 1909. p. 12.

theless the growth of the hypocotyls caused me much
trouble even here. Therefore as soon as the atmospheric
temperature permitted it, I put the growing-boxes out of
doors and then I always had quite straight seedlings. This
last point is the strongest argument in favour of my idea,
that want of fresh air was the cause of all my trouble.
During the growth in the hothouse or in the dark room
the temperature was registered by means of a thermograph.
Nearly always the temperature varied between 18° C. and
22° C., a few times only it was higher and then for a
short time only.

§ 6. Apparatus and dark room.

THE THERMOSTAT.

The special requirements to be fulfilled by a thermostat
fit for this investigation, were the cause that not one of
the existing types could be used. Therefore a new ther-
mostat constructed [1]) according to my specification was
obtained by the Botanical Laboratory of the University
of Utrecht. The extraordinary kindness and liberality of
Professor Went, who put a sum at my disposal from the
grant of the laboratary made it possible to give the
thermostat all the qualities I thought necessary for my
experiments.

The manner of heating and the regulation of the tem-
perature were imitated from the apparatus used in the
van 't Hoff-laboratory at Utrecht. [2]) To the mechanician
of that laboratory, J. W. de Groot, I owe much helpful
information. The requirements which the thermostat had
to fulfill were the following:

1) The thermostat was constructed by D. B. Kagenaar sr.,
van Wijckskade, Utrecht. The total cost was about 200 guilders,
thermoregulator, stirring apparatus and lamps included.
2) A description of this apparatus is to be found in C. Euwen.
Piëzochemische onderzoekingen. Diss. Utrecht. 1910.

1. It must be possible to keep the temperature constant to within 0.1° C. at least during a long period without control.

2. The temperature must be quite uniform throughout the thermostat.

3. No gas may be used for heating. [1])

4. It must be possible to open and shut the thermostat quickly without losing much heat.

5. It must be possible to ventilate the thermostat. [2])

6. It must be possible to rotate an axle running through the thermostat from the outside so as to render it possible in experiments on geotropism to put the plants inside at any desired angle without opening the thermostat.

7. It must be possible to use the thermostat in experiments on phototropism and therefore it should have a glass front and a sufficient depth to ensure a sufficient falling off of the intensity of the light. [3])

In order to satisfy these seven requirements the thermostat had to be different from the current types used in botanical laboratories, in the first place the method of closing. The ordinary arrangement with a double door always causes a difference of temperature of several tenths of a degree between the front and the back of the thermostat. Hence I took as base (cf. fig. 3 and plate I) an inner vessel A, which can be shut hermetically by means of a lid C with nuts, and which stands quite free in a larger vessel B, filled with water, so that the inner vessel is surrounded by it on all sides. Two stirrers D D placed in the left front-corner and in the right back-corner keep the water moving. They were provided with a straight vertical blade to the full height of the thermostat and

1) cf. § 8, purity of the air.
2) cf. § 7, purity of the air.
3) In the beginning it was my intention to extend this investigation to phototropism too. From lack of time I had to confine myself to geotropism.

were driven by an electromotor at a speed of 200 revolutions per minute.
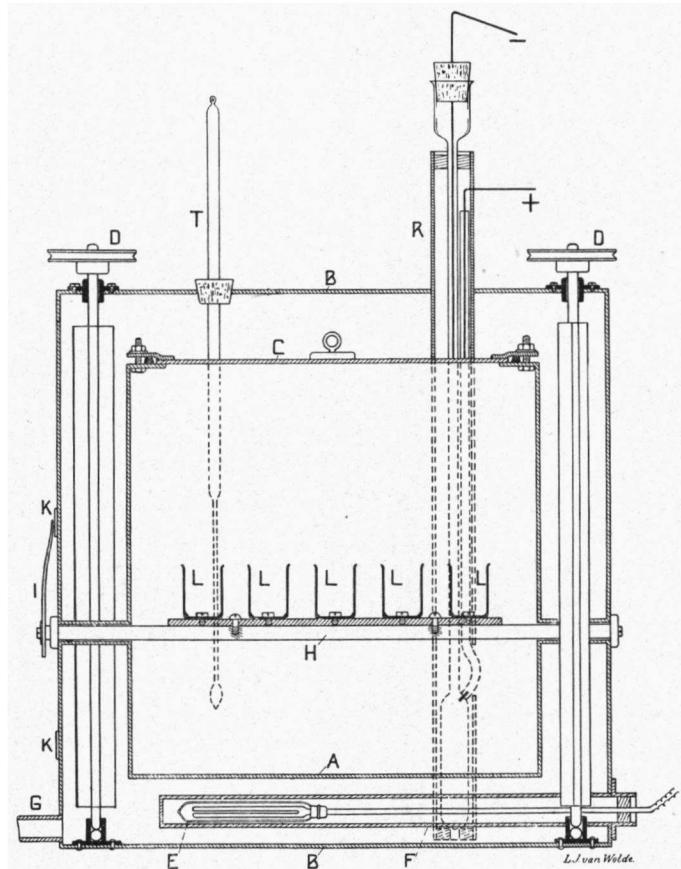

Fig. 3. Scale 1 : 5.
Dimensions 40 × 40 cm.

The outer vessel had a width of 40 cm., a height of 40 cm. and a depth of 60 cm. The dimensions of the inner vessel were 30 × 30 × 50 cm.

In the second place heating by gas was excluded and

therefore electricity was made use of. Four incandescent
lamps E in copper tubes F in the water-jacket under
the inner chamber were connected to the laboratory main.
Only one of these four lamps is shown in the figure. The
regulation of temperature also took place by means of
electricity. The thermoregulator R (cf. fig. 4 and the special
description) consisted of an open thermometer with a large
mercury-reservoir and a wide capillary in which a platinum-
wire could be pushed up and down; this wire made contact
with the rising mercury when the temperature had risen
to the desired point.

This regulator (cf. plate I) was connected to a couple
of accumulators, a resistance-box and a switch, which
automatically interrupted the electric current of the lamps
as soon as the temperature and with it the mercury
had risen sufficiently to close the circuit through the
accumulators. The accuracy of this apparatus left nothing
to be desired. The mercury of the regulator rose 6
m.m. for a rise of temperature of one degree C., and
so it was quite easy to adjust by hand the platinum
wire so that the temperature remained constant to 0.1° C.
In order to open the thermostat it was necessary to
lower the level of the water about 5 cm. so that the
lid C of the inner chamber became visible. To prevent
a loss of heat the water was run into a second vessel
by means of a wide tube G, entering the outer vessel
near the bottom. The latter could be moved up and down
by means of two pulleys in the ceiling, which made the
water flow up or down; it was constructed on the prin-
ciple of a hay-box, which made the loss of heat only very
small. As the outlet was wide and the round lid (which
took up a little more than half the top wall of the inner
vessel) was fastened with six nuts only, the opening and
closing took only a few minutes; hence the fall of tem-

perature was but some tenths of a degree and was overcome very soon afterwards.

To be able to ventilate without disturbing the thermal equilibrium in the inner vessel, two long spirals of metal tubing were placed in the water-jacket between the inner- and outer-vessels. These spirals (which are not reproduced in fig. 3) served to ventilate the thermostat. The air used came directly from the roof by means of a pipe and an airpump worked by water-power caused a continuous circulation. Some water always remained at the bottom of the inner vessel so that the latter was saturated with vapour.

An axle H, with indicator I and graduation K on the side-wall of the outer-vessel, could be rotated from the outside. It turned in two cylindrical cases, soldered watertight in opposite side walls between the outer- and inner-vessels. On this axle was screwed a copper plate, on which were five clamps L, so that plants in 5 vessels could be stimulated simultaneously. In view of the experiments on phototropism the inner vessel measured 50 cm. from front-wall to back-wall; the front-walls of the inner- and outer-vessels were of thick plate-glass, and the back-walls could be taken off to determine the absorption-coefficient of the front-wall. The whole apparatus was made of copper, and whereever the copper came in contact with the water, the surface was coated with tin.

THE THERMOREGULATOR (cf. fig. 4).

The thermoregulator also was constructed according to the indications of Mr. de Groot, mechanician of the van 't Hoff laboratory. The regulator consists of an open thermometer with a large mercury-reservoir A and a wide capillary B with a thick wall. The regulator used by me had a bulb of $2^{1}/_{2}$ cm. diameter and 10 cm. height. Into the reservoir A a platinum-wire had been fused, which

opened into the joint tube C, where the wire was in contact with mercury, which in its turn was in contact with the wire K, which is continually immersed in the mercury.
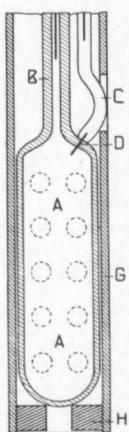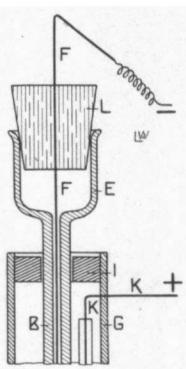
In the thick-walled capillary B, opening at the top in a glass funnel E, the platinum-wire F, passed through the cork L, can be pulled up and down to adjust the regulator at a definite temperature. The wire F is connected with the other pole of the accumulators, with which the resistance-box and the interruptor, for breaking the main current are also connected.

The regulator as a whole is covered by a mantle G with logs H and I in order to support the glass-frame. At the height of the mercury-reservoir four rows of openings in the copper jacket are made.

THE DARK ROOM.

All experiments took place in the dark room of the Botanical Laboratory at Utrecht; this dark room has been used exclusively for experiments on geotropism and phototropism, during the last few years. The area of this dark room is 3×3 metres, its height is $4\frac{1}{2}$ metres, it is wholly painted dead-black inside. The gasmain has been out of use for several years, but the room has one permanent electric light and there are three switches available. A double door with half a meter space between the two doors makes it possible to enter or to leave the room without any light entering.

Fig. 4. Scale 1:2,6. Total height 50 cm.

In the ceiling an electric fan is placed above a case of black cloth, so that the room could be aired quite sufficiently in a short time.

As the dark room is situated in the centre of the building, sudden changes in the temperature out of doors were felt only very slowly. Moreover a small steam radiator could be used, while on the other hand the fan together with spraying in the room and the space between the doors with water made it possible to keep the temperature of the room some degrees below the temperature of the building if desired.

During winter the room was kept damp by watering once or twice a day, later on even this was unnecessary as the water of the thermostat and of the water-current, which worked the air-pump, were sufficient to keep the room damp. At each experiment I noted the humidity of the room measured in degrees of a hygrometer, which had previously been checked at the points 0° and 100°. Of course this way of measuring was rather a rough one, but it was sufficient for my purpose. I tried to keep the humidity at 70° or higher, seldom it was below 60°.

§ 7. Sources of error.

As it was my purpose in this investigation to obtain results quantitatively as trustworthy as possible, I bestowed particular care on the tracing of all sources of error and on their elimination. The first four months of the investigation were taken up almost entirely with this and the first 300 experiments (of which a few only are mentioned in this paragraph) were used almost exclusively to get a clearer insight into these difficulties.

The results of this preliminary investigation form the contents of this section. For the sake of convenience

I give the different points, spoken of here, under three headings: firstly the sources of error due to the experimental object, in the second place those inhaerent in the experimental conditions and lastly the personal error of the observer.

A. SOURCES OF ERROR DUE TO THE EXPERIMENTAL OBJECT INDIVIDUAL VARIABILITY.

Repeated mention has already been made of individual variability as one of the most dangerous sources of error.

Rothert [1]) in discussing his method says amongst other things the following: „Die Krümmungsfähigkeit variïrt nicht nur sehr erheblich mit der Entwickelungsphase der Objecte, sondern sie ist auch bei gleicher Entwickelungs-phase individuell in weiten Grenzen variabel; . . . . zur Erziehung zuverlässiger Werthe ist es daher erforderlich, in jedem einzelnen Versuch nicht nur mit möglichst gleichartigen, sondern überdies mit möglichst zahlreichen Objecten zu experimentiren."

Nevertheless the number of plants, with which he worked („jede Gruppe umfasste in der Regel 4—10 Exemplare") was too small to guarantee him against errors, caused by the occurrence of extreme variants.

Bach [2]) gives the same opinion on this subject: „In allen meinen Untersuchungen, legte ich grossen Wert darauf, sie auf eine möglichst umfangreiche Zahl von Versuchen auszudehnen, denn nur durch diese statistische Methode können, wie die Erfahrung lehrt, die sehr stören-den, nicht ausschaltbaren individuellen Verschiedenheiten der einzelnen Versuchspflanzen derselben Art ausgeglichen werden."

According to this Bach usually took a much larger number of plants for each experiment than Rothert did.

1) W. Rothert, 1894, p. 12.
2) H. Bach, 1907, p. 58.

Thirdly the results of Mrs. Rutten—Pekelharing [1]) made me foresee difficulties on this point. Mrs. Rutten—Pekelharing had been working in the same laboratory under the same conditions and with the same object of experiment; the following tables compiled with the aid of the figures on page 261—266 of her investigation show how far variability made itself felt:

Angle of deviation 90°.

Temperature.	Number.	Curved.	Percent.	Duration of stimulation.
22°.5	12	12	100	4'36"
23°.5	12	6	50	4'36"

Angle of deviation 45°.

Temperature.	Number.	Curved.	Percent.	Duration of stimulation.
24°	12	12	100	6'5"
24°	13	6	46	6'6"

Angle of deviation 135°.

Temperature.	Number.	Curved.	Percent.	Duration of stimulation.
23°	13	8	61	5'42"
23°	13	7	54	5'40"
23°	11	5	45	5'42"

Angle of deviation 40°.

Temperature.	Number.	Curved.	Percent.	Duration of stimulation.
24°	12	10	83	7'11"
24°	14	7	50	7'21"
23°	15	0	0	7'

I too thought statistical treatment the best means of overcoming this difficulty. Therefore in the beginning I

1) C. J. Rutten—Pekelharing, 1910, p. 261—266.

used 100 plants for each experiment, but soon I had to
diminish this number to 50 and even later to 25, because
I could not otherwise obtain a sufficient number of expe-
rimental .objects.

There is however a second way of avoiding this diffi-
culty or at least of minimizing the influence of variability
on accuracy, and this second way has been of more help
to me than increasing the number of experimental objects.
The deviations from the average, here taken together
under the heading individual variability are caused for
the greater part if not wholly by differences in the external
conditions, the purity of the atmosphere perhaps in the
first place. The amplitude of the variability would be
much smaller, if it should be possible to eliminate these.
Acting according to this line of thought I have been
fairly successful in limiting the variability, at least my
figures show much greater concordance than those of
Mrs. Rutten-Pekelharing, and this greater concor-
dance cannot be wholly ascribed to the larger number of
plants used.

NUTATIONS.

At the end of his discussion of the nutations of *Avena*
Rothert says:[1] „Eine erschöpfende Untersuchung der
Oscillationen lag nicht in meiner Absicht; ich habe die-
selben nur darum berücksichtigen müssen, weil sie bei
meinen heliotropischen Versuchen eine Quelle von Täu-
schungen bilden konnten und mich anfänglich auch
thatsächlich irre führten". These words — including the last
ones — I can adopt with regard to my geotropic experi-
ments and they account for the observations following here.

At first I attempted to note down as a positive result
every „just perceptible curvation." Proceeding in this way

1) W..Rothert, 1894, p. 33.

I found presentation-times considerably shorter than those observed by Mrs. Rutten-Pekelharing in the case of experiments made under the same conditions and with the same plant. Distrusting these results I made control-experiments and I asked some one else to stimulate some vessels only among a number of marked vessels, of which I had then to observe the reaction. The result was that even in the non-stimulated vessels I observed curvations, in one case even 30 percent. After this experience the „just perceptible curvation" had to be more obvious, should I note down a positive result. Having made a number of experiments relating to this point I thought myself able to distinguish pretty surely the geotropical curvation from the nutation, although I did not neglect the possibility of mistakes on this point.

Later experiments proved the necessity of more decisive measures.

These experiments plainly showed that when the negatively geotropical reaction subsides an opposite reaction occurs. Generally this was a feeble reaction of 5—15 % of the plants only, although here a distinct curvation of the top was seen, which quickly disappeared again. As sometimes these curvations were seen several times in succession in 25—80 % of the plants, it became necessary, to trace the cause of this phenomenon. Further consideration of the figures, and observation of the reaction during several hours and the behaviour of non-stimulated plants induced me to look for an explanation in vigorous autonomic nutation. [1]) Hence we have to consider the nutations

1) When occupying myself with this phenomenon, I happened to read a paper by E. Pringsheim Jr., (1909) on phototropism, in which a similar experience is described in the case of phototropism. Pringsheim decides in favour of a real negatively heliotropic reaction. My opinion is that in the case communicated by him the explanation has also to be sought for in nutations.

of *Avena* somewhat more in detail. Rothert[1]) states, that the nutations of *Avena* do not always have a period of the same length; from his figures on the oscillations in the heliotropic curvation after 3½, 5, 6½ hour a period of about 180 minutes can be deduced. Rothert mentions further, that more than once he observed the coleoptile completing a rectilinear course of 1 cm. in 60 minutes, which observation quite agrees with my own experience and points to a period of about 120 minutes.

The direction of the most vigorous nutation is always the same with regard to the bilaterally symmetrical structure of the coleoptile. The coleoptile indeed is not circular at the top, but elliptical and the main direction of nutation is in the plane of the minor axis of this ellips. As I always planted the germinated oat-grains parallel to each other, I had ample opportunity of comparing nutation in both directions. When gravitation was acting in the direction of the minor axis of the ellips (which at the same time is that of the main axis of the grains), I found the presentation-time shorter than in other cases (vide infra, position of plants); therefore all preliminary experiments (series A and B) were made with plants in this position. Later, after the above-mentioned experiences I always made gravitation act in the direction perpendicular to that of the most vigorous nutation. (series C).

Taking this information into account we can easily explain these reversed curvations as nutations. For this purpose I give the figures of a striking case move fully, quoting from the protocol of my experiment:

B experiment 75. Date: 18—II—1910.
Stimulation-time: 4'40". Temp: 20° C.
Not in the thermostat.

1) W. Rothert, 1894, p. 27—33.

Number: 21.   Curved after:

30 minutes	: 11 —		35 min.	: 17 —		40 min.	: 21 —		
45	„	: 21 —	50	„	: 14 —	55	„	: 6 —	
60	„	: 1 — ? 11 + ?	65	„	: 1 — ? 10 +	70	„	: 1 — ? 17 +	
75	„	: 1 — ? 17 +	80	„	: 0 — 10 +	85	„	: 0 — 3 + ?	
90	„	: 3 — ? 3 + ?	95	„	: 3 — ? 0 +	100	„	: —	
105	„	: —	110	„	: —	115	„	: —	
120	„	: 0 — 8 +	130	„	: 0 — 10 +	140	„	: —	
150	„	: 0 — 5 +	160	„	: —	180	„	: 0 — 5 +	

The following points are worthy of notice:

1°. Percentage of curved (100 %) too high (normally 60—80 %).

2°. Reaction-time too short (30 min. instead of 36 min.).

3°. The reaction subsides with extraordinary rapidity.

4°. After 70—75 min. reaction vigorously positive.

5°. Positive reaction subsides rapidly.

6°. Reaction oscillating, after 40 min. maximum of negative reaction, after 70 min. maximum of positive reaction, after 95? min. negative again, after 120—150 min. positive again.

This tallies exactly with the supposition that the geotropic stimulation has taken place exactly at the moment, that the nutating coleoptiles were vertical and were on the point of starting a curvature in the same direction as would be induced by the negatively geotropic stimulation.

Suppose the nutation-period to be 70 minutes — and Rothert's figures do not conflict with this supposition, as he himself gives various values for this period —, then we find, calculating where the maxima of positive and negative curvation are to be seen:

Maximum.		Maximum.	
calculated from nutations		observed	
negative	35 min.	40	min.
positive	70 „	65—75	„

negative   105 min.   '95 ?   min.

positive   140   „   120—150   „

The agreement between observed values and the calcu-
lated ones is as striking as could be expected.

The supposition that we have nutations here, explains
fully the above mentioned six points, and I cannot see
how point 6 could be susceptible of any other explanation.
Two questions only remain unanswered : first, why these
curvations in opposite direction have been seen in some
experiments only and further, why nearly all the seedlings
were nutating in the same direction.

With regard to the first point I look for an explanation
in the fact that these curvations became obvious as soon
as the atmosphere in the dark room became purer; this
quite agrees with our knowledge concerning nutations. [1]
The circumstance, that I observed them, but rarely finds
an explanation in the fact, that this phenomenon can
appear only when stimulation lasts for a period slightly
longer than the presentation-time; moreover I have excluded
these phenomena on purpose in series C. as I have stimu-
lated in a direction perpendicular to the main direction
of nutation.

The second question I cannot answer. The nutation at
the same moment and in the same direction of a set of
plants grown together — a fact mentioned by Rothert [2]
too — points to the conclusion that nutations are not so
perfectly autonomous as they are generally believed to be.
The geotropic curvation thus presents itself at first as an
increased nutation of definite direction, in agreement
therefore with the views of Darwin [3]), who reckons the

1) O. Richter, 1909, p. 488.
2) W. Rothert, 1894, p. 32.
3) Ch. and F. Darwin, 1880.

phototropic and geotropic phenomena among the modified nutations.

HEIGHT OF PLANTS.

The length of the *Avena*-coleoptiles has no influence upon the magnitude of the geotropic presentation-time, provided that the dimensions of the coleoptiles lie between 10 and 35 mm. This was verified by preliminary experiments made for this purpose and agrees perfectly with the results of Blaauw [1]) as to the phototropic presentation-time.

AGE OF PLANTS.

With a single exception only plants of 4 days old were used; the seeds were soaked for two of these four days and were then grown in the zinc vessel for 2 days more. Plants of 5 days old were used exceptionnally. A series of preliminary experiments showed no difference between plants 4 days old and others 5 days old.

POSITION OF PLANTS.

Rothert [2]) says, speaking of the direction, in which the coleoptile is stimulated: „Trotz seiner deutlich dorsiventralen Structur verhält sich die Cotyledo [3]) physiologisch wie ein radiäres Organ; wenigstens beobachtete ich keine merklichen Differenzen der Krümmungsfähigkeit in Abhängigkeit davon, welche Seite des Cotyledo der Lichtquelle zugekehrt war." Blaauw [4]) too regards the coleoptile of *Avena* „physiologically" circular. This however is not quite the case, although the difference is only a slight one.

The geotropic presentation-time was found a little shorter when stimulating in the direction of the short axis of the elliptical apex than in a direction perpendicular to

1) A. H. Blaauw, 1909, p. 12.
2) W. Rothert, 1894, p. 30.
3) So the coleoptile is named by Rothert.
4) A. H. Blaauw, 1909, p. 11.

this. Thus I found the following differences: A experiments
201—212, 171 seedlings, of which 42 curved, i. e. 25 % in
the second case, and 142 seedlings, of which 83 curved,
i. e. 58 % in the first case. In the same way B experi-
ments 78—81, of 50 seedlings 19 curved i. e. 38 % in the
second case and of 50 seedlings 24 curved i. e. 48 % in
the first case. Probably this phenomenon is connected
with the much stronger nutation in the plane of the higher
percentage of curved seedlings.

This difference could not be a source of error as all
seedlings used in the experiments were in parallel positions.

PRELIMINARY TREATMENT OF PLANTS.

Bach [1]) proved, that a stay of some hours at 4° C.—
10° C. had a real influence on the magnitude of the pre-
sentation-time, even when the plants were stimulated
1½ hours after being transferred to 20° C. On account of
this statement I at first attached great value to growing
the plants at as constant as possible a temperature. Later,
when it became evident, that the influence of small dif-
ferences of temperature was quite lost during the first hour
of preliminary warming I did not exclude slight differen-
ces, taking care only, that the experimental plants passed
the hours immediately preceding the experiment at a
temperature, differing from 20° C. by not more than a
few degrees.

B. SOURCES OF ERROR, CAUSED BY EXPERIMENTAL CONDITIONS.
PURITY OF THE ATMOSPHERE.

Richter [2]) has the merit of having traced in detail
the influence of impurities in the air upon physiological
processes and of having emphasised the fact that they
constitute a very dangerous source of error.

1) Bach, 1907, p. 72, 76.
2) O. Richter, 1909 and 1906 and the literature quoted there.

From the beginning I attempted to avoid this danger. In the dark room the gas-main was turned off permanently. The thermostat was heated electrically. Moreover, the dark room was ventilated several times a day, by means of the electric fan, the fresh air being obtained from the spacious rooms and corridors of the laboratory, where no gas was burned either, as the whole laboratory is lighted electrically. The air passing through the thermostat itself came directly from the roof of the laboratory.

In this way I thought sufficient precautions had been taken against any impurity of the atmosphere, in which I had to make my experiments, but experience has taught me not to be too readily satisfied in this respect.

The thermostat was the Trojan horse, which brought in the bad vapours unnoticed. As a warning to others I will describe my experiences on this point somewhat more fully, especially because this source of error has in the aggregate detained me at least for one month.

In the last days of December 1909 the thermostat arrived; it was constructed of copper, the inside was covered with tin and the outside painted and at that time I began to work in the thermostat in the dark room.

Before leaving on January 1st 1910 for a ten days' holiday I made some preliminary experiments at 20° C., 25° C. and 30° C., after a preliminary warming of 1 hour.

Resuming my experiments on January 15th I could not succeed in getting the same presentation-time at 30° C., which I had found on December 31st. I thought of every possible disturbing influence which could make itself felt inside the thermostat, I thought of phototropism, of hydrotropism, of aërotropism, of thermotropism, but not one of the experimental variations I tried could throw light on the cause of my failure. At last I was quite certain that the cause was not any polarity of my apparatus.

Then I tried outside the thermostat in the dark room, stimulating 4'30" at 20° C. (which is more than the presentation-time at 20° C.) and found that of 70 seedlings not a single one curved. Now either the condition of the dark room or that of the seedlings was necessarily the cause. In order to settle this I made several experiments in the dark room of the hothouse and there the reaction was very good. So it was evident that the dark room constituted a bad influence and now for the first time I thought of the paint of the thermostat and perhaps of other parts too, which might spoil the air of the dark room when heated. The thermostat was emptied and heated on a stove with a permanent fire, for a week, during which time I investigated whether the air in the dark room was improving.

The success was complete: On February 10th the thermostat (which had then been in use for two months) was removed from the dark room and the same day the electric fan was worked for half an hour. On February 11th ventilation by means of the electric fan was started at 9 o'clock in the morning; at 10.15 a batch of plants was stimulated during 4'30", result: 36 % curved; the ventilation was continued until 3.35, when a second batch of plants was stimulated during 4'30", result: 74 % curved. Hence it was out of the question, that the dark room had been spoiled by the thermostat and that the ventilation had rectified it again.

After these experiments I always used the electric fan freely; and moreover made regular control-experiments in order to discover any impurity of the air.

These control-experiments proved at the same time that the heating of the thermostat had been a sovereign remedy, for a decrease of the reaction-faculty of the

experimental · objects caused by the stay in the room
never occurred afterwards.   ·

Of course the atmosphere in the dark room was not
absolutely pure; absolute purity is not to be attained in
a laboratory; but I felt fully satisfied, if the air was as
pure as the conditions of my work would allow, and if
the remaining impurities had a constant influence without
making a comparison between the results impossible.

As has been mentioned above, the atmosphere in the
dark room was thought to be pure, when the presentation-
time at 20° C. amounted to 4'20". Later on this changed:
after May 18th the presentation-time at 20° C. decreased
to 3' (cf. tables VI and VII at 20° C. in Chapter II).
I feel pretty sure this has to be attributed to the fact, that
the building was not being heated any more after that
date, and was ventilated much better than in winter.
Perhaps also the fact was of some influence that from
February to May the thermostat was heated day after
day; after the 18th of May on the other hand it was cooled
in order to work at low temperatures. As my starting-
point was the presentation-time of 4'20" at 20° C., I have
multiplied the presentation-time of all further observations
(since May 18th) by $^{13}/_9$, by which means these results
became comparable to those obtained before May 18th.

That the presentation-times at all temperatures were
changed in the same way by this alteration in the external
conditions was proved by comparing not only experiments
at 20° C. before and after May 18th, but also experiments
at 0° C. The first determination at 0° C. was made from
February 26th to 29th, the second from June 17th to 20th.
In the first case the presentation-time was 72', in the
second one 48' and $^{13}/_9 \times$ 48' = 69'20". The agreement
between these values is very striking, when we take into
account the fact, that the first determination was made

out of doors in melting snow, the second one in the
thermostat, which easily · could have caused a slight
difference.

In the case of the experiments out of doors in the
melting snow the seedlings were influenced also by the
impurities of the laboratory-atmosphere, as the stay out
of doors was of short duration only and even during that
time the wooden boxes in which the plants were placed
out of doors, were filled with the air of the dark room.

Without any hesitation I therefore accepted the factor
$^{13}/_{9}$ as applicable to all temperatures. By ascertaining the
fact, that my starting-point (the presentation-time at 20° C.
up till May 18th 4'20", after that date 3') remained con-
stant, I could finally bring together all values as being
directly comparable.

TEMPERATURE.

Temperature. plays a very small part as a source of
error in this investigation. As has been said above, the
thermostat could be kept constant to 0.1° C. In the be-
ginning this was done only in cases, in which the plants
remained in the thermostat for less than 6 hours; the
stirring-apparatus was stopped during the night, when
the temperature remained constant to 0.3° C. Later the
stirring-apparatus was also kept running during the night
when necessary. At 35° C.—40° C. all figures refer to a
temperature regulated to 0.1° C.

The same thermometer, with a scale divided to 0.1° C.,
was used in all experiments. In the course of the inves-
tigation this thermometer was compared with a thermo-
meter in the Physical Laboratory, graduated to 0.05° C.

In view of possible errors it was of much importance
to know the exact course of·the temperature within the
thermostat when heating.

To trace this I made some thermo-electrical determinations

in the Physical Laboratory. In the first place the time needed to bring the air inside the thermostat to a certain temperature was determined, and secondly what time the mould inside the vessels needed for this purpose. The coleoptiles of *Avena* were too small to use these for the experiment.

When the difference of temperature between the water of the thermostat and the mould in the vessel was 15° C. at the beginning, the air inside was at quite the same temperature as the water after 45 minutes, and the mould was still 0.4° C. behind after 45 minutes, and 0.1 C. after 60 minutes. As the coleoptiles are heated more slowly than the air, but faster than the mould, they were less than 0.1° C. behind the temperature of the water after one hour. In comparison with the sources of error from other experimental conditions this time of preliminary warming was quite sufficient. No experiments were made in which a shorter preliminary time was allowed.

HUMIDITY.

Nowhere has an influence of humidity upon the pre-sentation-time been noticed; but I must add, that this influence has not been investigated. On the contrary, I tried to keep the humidity as constant as possible and within the thermostat the air was always saturated with vapour, as part of the bottom was covered with water.

LIGHT USED.

All observations were made at the same place in the dark room and with the same red light. To this end an ordinary electric lamp was used, placed under a glass-bell after S a c h s, filled with a saffranin solution of 2 %₀. [1])

The constancy of the red light was no superfluous precaution as is shown by the following experiment. A set

1) cf. A. H. B l a a u w, 1909, p. 78.

of plants was observed in the light of the small red
electric lamp used for reading the thermometer, and
immediately afterwards the same set was placed near the
lamp under the glass-bell, (which gave a much stronger
light). In the first position I noted down 50 % curved, and
in the second one nearly 100 %. That this was not a
personal error, was shown by the fact that two other
persons who tested in the same way, also found the
seedlings curved with the aid of the saffranin-lamp to be
twice as many as by the smaller lamp.

C. SOURCES OF ERROR DUE TO THE OBSERVER.

The personal error only belongs to this heading and
it is a constant one and therefore left out of consideration.
It cannot be very great either, as my figures are perfectly
in harmony with those of Mrs. Rutten—Pekelharing.

A further small error may be introduced by the fatigue
of the eye, but the errors caused by this can never be
more than magnitudes of the second order.

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CHAPTER II.

RESULTS.

§ 8. The presentation-time at different
temperatures.

After all that has been said in the preceding chapter I
need not give further space to the methodical part of the
investigation. A few remarks only have to be made before
giving a survey of the figures obtained at different tem-
peratures.

As has been set forth in § 4, the results of the experi-
ments at a definite temperature and with a definite time
of preliminary warming were collected into one table.

Several tables were obtained in this way for each tem-
perature. Now all these tables are reproduced as appendix
at the end of this paper and every experiment may be
found there. They are not however suited to give a clear
idea of the alterations of the presentation-time as a
function of temperature and of time of preliminary war-
ming. To obtain this end the last columns but one of
these tables have been collected into one table for each
temperature. In this way the tables I—XIV were obtained
and follow here. To each of these tables belong the tables
with the same number in the appendix. Thus e.g. the
table IX owes its origin to the tables IX A, IX B, IX C,
IX D, IX E and IX F. These tables I—XIV give the per-
centage of curved plants at each temperature after a
varying duration of preliminary warming. At the bottom
of the columns, relating to a definite time of preliminary
warming, the presentation-time is given for the experi-
mental condition mentioned at the head of the column.

Two tables are given for 0° C. and for 20° C., as expe-
riments were made at these two temperatures before and
after the change in conditions, spoken of in § 8 B. The
tables I and II were used as well as VI and VII to fix
the factor $^{13}/_9$, by which the presentation-times at the
bottom of the tables III—V and XI—XIV had to be
multiplied.

In order to find the mean of the percentage of curved
plants the total number of plants has always been used.
Thus for instance, if the mean was to be found of two
experiments, one with 50 plants of which 15 curved
(i. e. 30 %), and another with 150 plants of which 75
curved (i. e. 50 %), the mean was taken as 90 of 200
(i. e. 45 %) and not the mean of 30 % and 50 % (i. e. 40 %).

TABLE I.
0° Centigrade.

Stimulation-time.	After 1 hour's preliminary warming.
885'	100 %
180'	97 %
90'	70 %
75'	59 %
60'	16 %
45'	0 %
30'	0 %
Presentation-time.	72'

TABLE II.
0° Centigrade.

Stimulation-time.	After 1 hour's preliminary warming.	After 4 hour's preliminary warming.	Mean.
60'	68 %	76 %	70 %
45'	52 %	33 %	45 %
30'	24 %	24 %	24 %
25'	0 %	0 %	0 %
15'	0 %	0 %	0 %
Presentation-time.	44'	51'	48'
Presentation-time × $^{13}/_9$.	64'	74'	69'

TABLE III.
5° Centigrade.

Stimulation-time.	After 1 hour's preliminary warming.	After 4 hour's preliminary warming.	Mean.
13'	60 %	58 %	59 %
11'	57 %	44 %	50 %
9'	46 %	36 %	41 %
Presentation-time.	9'40"	11'50"	11'
Presentation-time × $^{13}/_9$.	14'	17'10"	16'

TABLE IV.
10° Centigrade.

Stimulation-time.	After 1 hour's preliminary warming.	After 4 hour's preliminary warming.	Mean.
9'	78 %	—	78 %
8'	63 %	64 %	63 %
7'	45 %	46 %	45 %
6'	20 %	41 %	33 %
5'	24 %	—	24 %
Presentation-time.	7'20"	7'20"	7'20"
Presentation-time × $^{13}/_9$.	10'40"	10'40"	10'40"

TABLE V.   15° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 4 hours' preliminary warming.	After 24 hours' preliminary warming.	Mean.
7'	96 %	97 %	100 %	97 %
6'	72 %	79 %	97 %	81 %
5'	70 %	74 %	67 %	71 %
4'	46 %	46 %	45 %	46 %
3'	33 %	32 %	33 %	33 %
2'	0 %	0 %	—	0 %
Presentation-time.	4'10"	4'10"	4'10"	4'10"
Presentation-time. $\times$ $^{13}/_9$.	6'	6'	6'	6'

TABLE VI.   20° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 8 hours' preliminary warming.	Mean.
5'	—	88 %	88 %
4'40"	82 %	76 %	79 %
4'20"	52 %	56 %	54 %
4'	28 %	48 %	38 %
Presen-tation-time.	4'20"	4'10"	4'20"

TABLE VII.   20° C.

Stimulation-time.	After 1 hours' preliminary warming.
5'30"	93 %
5'	85 %
4'	73 %
3'	51 %
2'	20 %
Presentati-ontime.	3'
Presentati-ontime. $\times$ $^{13}/_9$.	4'20"

TABLE VIII.   25° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 2 hours' preliminary warming.	After 4 hours' preliminary warming.	After 6 hours' preliminary warming.	Mean.
4'	100 %	—	—	—	100 %
3'30"	92 %	83 %	86 %	100 %	89 %
3'	60 %	80 %	64 %	84 %	66 %
2'30"	55 %	56 %	60 %	60 %	59 %
2'	44 %	24 %	20 %	34 %	34 %
1'30"	20 %	16 %	16 %	56 %	27 %
1'	0 %	0 %	0 %	25 %	6 %
Presentation-time.	2'20"	2'20"	2'20"	2'20"	2'20"

TABLE IX.   30° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 2 hours' preliminary warming.	After 4 hours' preliminary warming.	After 6 hours' preliminary warming.	After 12 hours' preliminary warming.	After 24 hours' preliminary warming.
4'30"	95 %	—	—	—	—	—
4'	72 %	95 %	—	—	—	—
3'30"	50 %	82 %	100 %	96 %	94 %	—
3'	30 %	40 %	82 %	80 %	—	95 %
2'30"	—	32 %	74 %	68 %	85 %	—
2'	0 %	0 %	44 %	57 %	72 %	51 %
1'30"	—	—	30 %	32 %	42 %	47 %
1'	—	—	0 %	—	0 %	26 %
Presentation-time.	3'30"	3'10"	2'10"	1'50"	1'40"	1'40"

TABLE X. 35° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 2 hours' preliminary warming.	After 4 hours' preliminary warming.	After 6 hours' preliminary warming.	After 18 hours' preliminary warming.	After 24 hours' preliminary warming.	After 48 hours' preliminary warming.
7'	—	—	—	—	100.0%	90 %	89 %
6'	92 %	87 %	90 %	100 %	65 %	60 %	65 %
5'30"	100 %	95 %	76 %	—	—	—	—
5'	100 %	80 %	74 %	83 %	53 %	48 %	45 %
4'30"	85 %	65 %	67 %	—	—	—	—
4'	62 %	53%	50 %	50 %	28 %	30 %	30 %
3'30"	83 %	49 %	29 %	—	—	—	—
3'	60 %	28 %	17 %	31 %	19 %	30 %	—
2'30"	54 %	37 %	7 %	—	—	—	—
2'	24 %	22 %	10 %	14 %	—	—	—
1'30"	12 %	5 %	—	—	—	—	—
1'	0 %	—	—	—	—	—	—
Presenta-tion-time.	2'30"	3'30"	4'	4'	5'	5'	5'

TABLE XI. 37° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 2 hours' preliminary warming.	After 6 hours' preliminary warming.	After 24 hours' preliminary warming.
30'	100 %	—	—	—
25'	—	—	100 %	—
20'	—	87 %	84 %	68 %
15'	—	100 %	52 %	52 %
10'	80 %	46 %	32 %	33 %
9'	86 %	—	—	—
8'	92 %	—	—	—
7'	62 %	—	—	—
5'	29 %	—	—	—
Presentation-time.	6'30″	11'	15'	15'
Presentation-time × $^{13}/_9$.	9'20″	16'	21'40″	21'40″

TABLE XII.   38° C.

Stimulation-time.	After 1 hours' preliminary warming.	After 2 hours' preliminary warming.	After 4 hours' preliminary warming.	After 6 hours' preliminary warming.	After 12 hours' preliminary warming.	After 24 hours' preliminary warming.
300'	—	—	—	—	—	52 %
240'	—	—	—	—	—	52 %
180'	—	—	—	—	—	44 %
120'	—	—	—	—	—	16 %
100'	—	—	—	—	75 %	—
80'	—	—	—	—	—	0 %
75'	—	—	—	—	74 %	—
60'	—	—	—	—	65 %	0 %
45'	—	—	—	57 %	37 %	—
40'	—	—	100 %	60 %	—	0 %
35'	—	—	—	41 %	—	—
30'	100 %	92 %	64 %	24 %	22 %	0 %
20'	100 %	83 %	28 %	0 %	—	—
15'	96 %	60 %	—	—	—	—
10'	70 %	31 %	18 %	—	—	—
8'	52 %	36 %	—	—	—	—
5'	21 %	12 %	—	—	—	—
Presentation-time.	8'	13'20"	26'	37'	52'	240'
Presentation-time $\times$ $^{13}/_{9}$.	11'30"	19'10"	38'	53'	75'	347'

TABLE XIII.   39° C.

Stimulation-time.	After 1 hour's preliminary warming.	After 2 hours' preliminary warming.
60'	100 %	—
40'	83 %	66 %
20'	57 %	40 %
15'	—	13 %
10'	40 %	14 %
Presentation-time.	16'	28'
Presentation-time. × $^{13}/_9$.	23'	40'

TABLE XIV.   40° C.

Stimulation-time.	After 1 hour's preliminary warming.
210'	46 %
180'	50 %
120'	0 %
90'	0 %
60'	0 %
30'	0 %
20'	0 %
10'	0 %
Presentation-time.	180'
Presentation-time. × $^{13}/_9$	260'

§ 9. Summary of results.

The following table contains all presentation-times, found determined during this investigation. The horizontal rows give the presentation-times belonging to the temperature at the beginning of the row. In the vertical columns the presentation-times after the same time of preliminary warming are put down. The figures are those of the last horizontal rows of the tables I—XIV. They are all directly comparable with each other.

Summary of presentation-times.

Temperature.	After one hours' preliminary warming.	After 2 hours' preliminary warming.	After 4 hours' preliminary warming.	After 6 hours' preliminary warming.	After 12 hours' preliminary warming.	After 24 hours' preliminary warming.
0°	72'	—	72'	—	—	—
5°	16'	—	16'	—	—	—
10°	10'40"	—	10'40"	—	—	—
15°	6'	—	6'	—	—	—
20°	4'20"	—	—	¹) 4'10"	—	—
25°	2'20"	2'20"	2'20"	2'20"	—	—
30°	3'30"	3'10"	2'10"	1'50"	1'40"	1'40"
35°	2'30"	3'30"	4'	4'	²) 5'	5'
37°	9'20"	16'	—	21'40"	—	21'40"
38°	11'30"	19'10"	38'	53'	75'	347'
39°	23'	40'	—	—	—	—
40°	260'	—	—	—	—	—

The influence of the temperature and the time-factor is very clear here. From 0° C. up to 25° C. the presentation-time shows no alteration due to the time of preliminary warming. At 30° C. the presentation-time decreases when the preliminary warming is increased. From 35° C. to

1) After 8 hours' preliminary warming.
2) After 18 hours' preliminary warming.
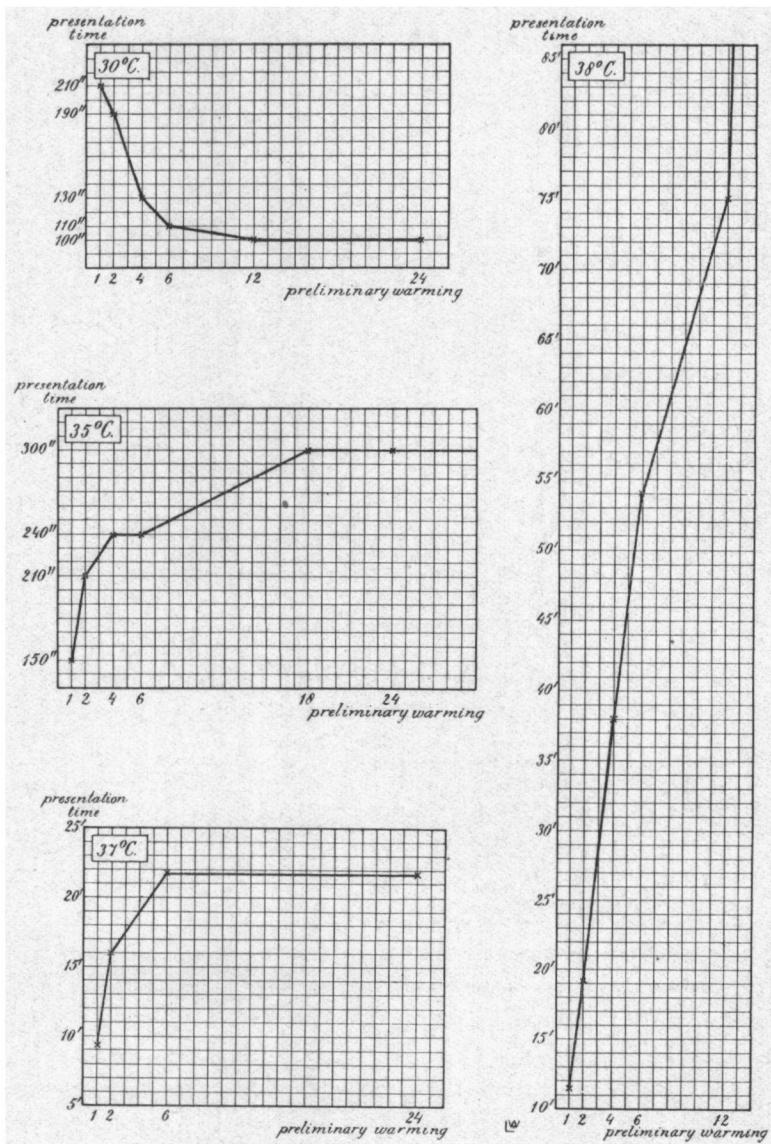
Fig. 5. Presentation-time at 30°, 35°, 37° and 38° C.

40° C. the presentation-time increases with a longer
duration of preliminary warming, and the more so when
the temperature is higher. Thus at 40° C. the presenta-
tion-time could only be determined after 1 hours' warming.

These results for the temperatures 30° C., 35° C., 37° C.
and 38° C. are represented graphically in Fig. 5. The
diagrams, given there, show very clearly the difference in
behaviour between the presentation-time at 30° C. and at
higher temperatures. The curve at 30° C. slopes down-
wards, those at higher temperatures upwards. The mea-
ning of this phenomenon will be discussed in Chapter III.

The widely divergent values of the presentation-time
make it impossible to give a diagram in which full jus-
tice is done to differences of some 10 seconds, while the
highest values found are also represented. Therefore such
a scale has been chosen in drawing Fig. 6 and 7, that
the small differences can be seen, but some of the highest
values are outside the diagram.

In Fig. 6, drawn after van Iterson [1]) the abscissae-
axis has been taken as temperature-axis, graduated to
1° C., and the ordinate-axis has been taken to represent
the presentation-time, graduated to 2 minutes.

From 0° C. to 25° C. we find only one value of the
presentation-time at each temperature, from 30° C. upwards
we find more values marked 1 to 6; the little crosses
numbered 1 are the values found after 1 hours' preliminary
warming, those numbered 2 after 2 hours', those num-
bered 3 after 4 hours', those numbered 4 after 6 hours',
those numbered 5 after 12 hours', those numbered 6 after
24 hours'. The broad black line represents the presentation-
time after 1 hours' preliminary warming, the thin line
starting from 25° C. the same after 12 hours' preliminary

1) G. van Iterson Jr. May 1910.
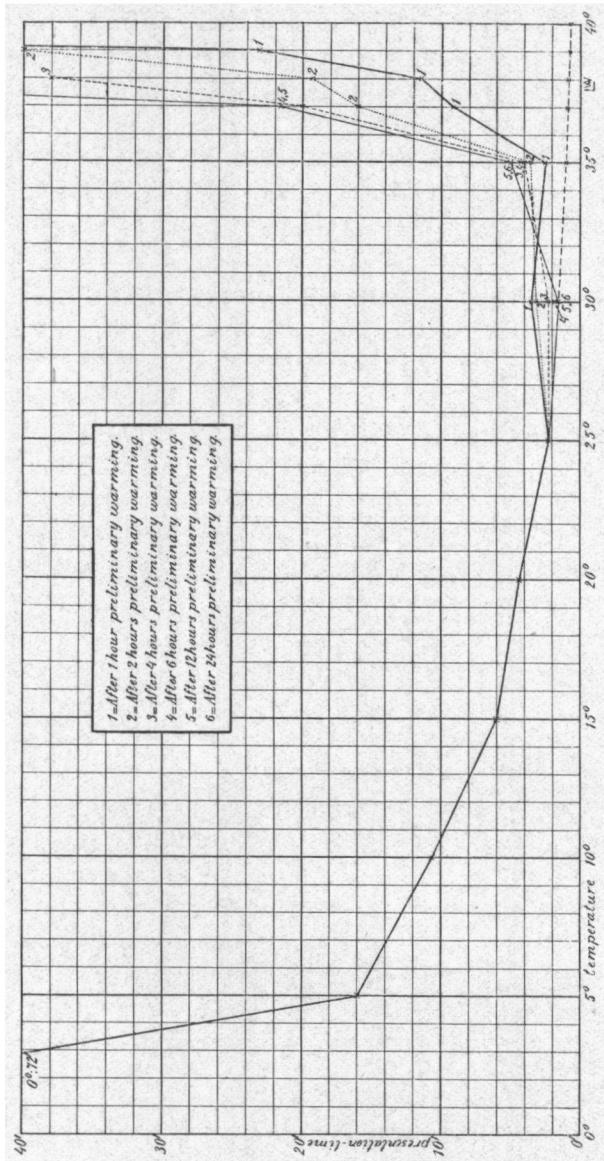
Fig. 6. The presentation-time in its relation to the temperature.

warming. Between these two lines we see a dotted line representing the presentation-time after 2 hours' and an interrupted one representing the same after 4 hours' preliminary warming.

The same figures are represented in Fig. 7 in a slightly different way, according to Blackman's diagrams. Here the values after different times of preliminary warming are put down in the diagram in such a way that at each temperature the values at that one temperature can be connected by means of a curve. Therefore the abscissae-axis is not only used as temperature-axis, but also as time-axis, so that at each definite temperature the hours' of preliminary warming are set down on the abscissae-axis beginning with the ordinate of the temperature concerned as starting-point. In other words the plane of the drawing is the plane containing the presentation-time axis and the temperature-axis. At each temperature between 30° C. and 40° C. another plane is needed containing the presentation-time axis and the axis of the preliminary warming-time. These last mentioned planes should be perpendicular to the first mentioned one and parallel to each other. Now, for convenience sake, these planes are turned down so as to be in the same plane as that of the drawing. In this way it has been possible to add to the diagram the curves A_0—A_6, B_0—B_6 etc., which represent the relation between presentation-time and time of preliminary warming at a definite temperature. It is only between 38° C. and 40° C. that some of these points lie outside the diagram. The scale, chosen for the time of preliminary warming determines whether or not the curves are very steep. Here the distance between two vertical lines has been made equal to 2 hours in order to get a diagram as comparable as possible to that of Blackman.

The conclusions, which may be drawn from the diagrams,
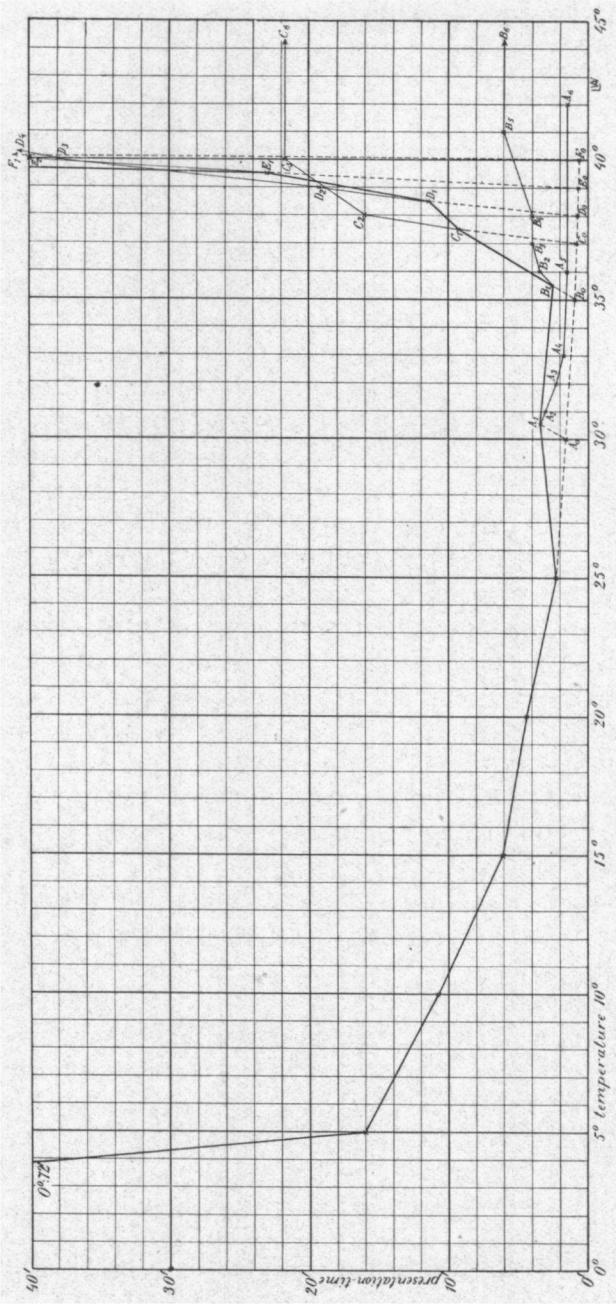
Fig. 7. The presentation-time in its relation to the temperature.

will be stated in Chapter III, where also Blackman's
ideas will be tested by the facts.

§ 10. Summary and discussion of reaction-times.

It was already pointed out, that in this investigation it
was not intended to trace the influence of temperature
upon the reaction-time. For this reason I am only able
to deal with this subject in.so far as my investigation
of the presentation-time has afforded figures dealing with
the reaction-time also.

The figures, given here for the reaction-time might be
supposed to be not quite accurate, as in all experiments
the plants were removed to a temperature of 20° C. before
the reaction-time was over. But this really does not make
a difference of any importance. At 5° C., 25° C. and 30° C.
the reaction-times were found nearly the same, whether
the plants remained at these temperatures after the pre-
sentation-time was over or were removed to 20° C.
Therefore I think these figures quite suitable for drawing
conclusions about the reaction-time.

I have taken as reaction-time the time elapsing from
the beginning of the stimulation till the moment that 50 %
of the seedlings showed a just perceptible curvation. These
values are to be found in the last column of the tables
in the appendix. A reaction-time has been mentioned
there also in the experiments, where only 40—50 % of
the plants were curved, although in that case there is
strictly speaking no reaction-time. In such cases the time
elapsing from the beginning of the stimulation till the
moment the maximum number was curved has been
taken instead of the reaction-time.

The following table gives a summary of a part of the
reaction-times found in this investigation. I did not think

it suitable to bring them all together in one table, because differences can only be traced when looking at special groups, and dividing these sufficiently under different headings.

I have therefore selected from the tables in the appendix all reaction-times relating to cases, where 40—60 % were curved (the cases, where the stimulation-time was nearly equal to the presentation-time) and those, where 90—100 % were curved (the cases, where the stimulation-time was sufficient to make all seedlings curve). For these two groups I calculated the average reaction-time at each temperature and the values obtained in this way are set down in the following table.

Summary of reaction-times.

Tempera-ture.	Experiments with 90—100 % curved.		Experiments with 40—60 % curved.	
	Reaction-time.	Number of plants used.	Reaction-time.	Number of plants used.
5°	—	— —	63'	224
10°	—	—	49'	378
15°	36'	142	49'	206
20°	36'	145	51'	338
25°	36'	261	43'	195
30°	36'	361	57'	537
35°	38'	364	54'	677
37°	41'	107	58'	119
38° [1]	43'	138	64'	112

1) The experiments where the stimulation-time exceeded 50 min. are left out of consideration.

Two things are very obvious from this table:
1°. that the reaction-time is not dependent upon tem-
perature between 10° C. and 35° C.;
2°. that the reaction-time is longer when stimulating
during the presentation-time than it is after longer
stimulation.

These conclusions are not in harmony with the results
of Bach.[1] He found the reaction-time as well as the
presentation-time both dependent upon temperature. As
to *Avena* this is certainly not the case; with regard to
Vicia Faba, the figures given by Bach are not sufficient
to prove it, because it is not possible to deduce from his
figures, whether or not the results obtained after different
stimulation-times have been sufficiently differentiated.

When comparing the reaction-times after different sti-
mulation-times Bach has surely put together values that
should have been kept separate. His groups are too large,
and the number of objects in each group is too small,
and therefore the difference in the reaction-times after
different stimulation-times has been overlooked.

My results concerning reaction-time are more in harmony
with Czapek's results,[2] who found the same value for
the reaction-time at 15° C., 20° C. and 25° C.

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1) H. Bach, 1907, p. 79.
2) F. Czapek, 1898.

CHAPTER III.

DISCUSSION OF RESULTS.

§ 11. Comparison of the results with those of previous investigations.

In § 2 a survey has been given of the dbservations of the influence of temperature upon geotropism, which have been published up to the present. In the first place the results obtained by Czapek and Bach mentioned there must be compared here with my own results.

Czapek [1]) used germinating roots of *Lupinus albus* and found, that the presentation-time did not depend upon temperatures between 15° C. and 80° C., that it rose slowly at higher temperatures and increased rapidly below 15° C. Bach [2]) on the other hand, using seedlings of *Vicia Faba*, found, that between 14° C. and 85° C. temperature had a constant, distinct influence upon the presentation-time, causing it to diminish between 14° C. and 80° C., and to increase slowly at still higher temperatures.

As to my own results, the table in § 9 shows very clearly, that from 0° C. to 30° C. the presentation-time continually decreases, and at higher temperatures it increases slowly at first and later more rapidly.

These results concerning presentation-time are generally in harmony with those obtained by Czapek and Bach, yet it remains an open question, why Czapek did not find a decrease of the presentation-time between 15° C. and 30° C. It may be that the explanation lies in the

1) F. Czapek, 1898.
2) H. Bach, 1907.

theory of limiting factors; in § 15 this point will be discussed in .detail.

The figures of Czapek and Bach, quoted in § 2, do not allow of any conclusions about the validity of van 't Hoff's law. The series of observations is not sufficiently complete nor is the accuracy sufficient for this purpose. Nevertheless there are some indications that the presentation-time is 2 to 3 times shorter for each rise of temperature of 10° C. Thus we can calculate from Czapek's figures: $Q_{10} = \frac{K_5}{K_{15}} = \frac{45'}{20'} = 2.25$, and from Bach's figures: $Q_{10} = \frac{K_{20}}{K_{30}} = \frac{7'5}{2'} = 3.75$. These values are not necessarily opposed to van 't Hoff's law, when we consider the way in which they are obtained.

Haberlandt's experiments [1]) with objects grown at very low temperatures, and those of Francis Darwin [2]) with plants exposed to high temperatures aimed more especially at gathering facts in support of the statolith-theory. As I did not occupy myself with this theory, there are a few points only, where there can be question about agreement or disagreement with the results of these investigators. Agreement is to be seen in so far as in the case of *Avena* the presentation-time is also lengthened by a stay at exceedingly high or low temperatures. Disagreement appears in the fact, that here even after a stay of 15 hours at 0° C. (experiment B 24, table I A) the faculty of geotropic curvature was not lost, as was found by Haberlandt in a similar case.

A comparison of the results relating to the reaction-time has already been made in § 10.

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1) G. Haberlandt, 1902 and 1903.
2) F. Darwin, 1903.

§ 12. Van 't Hoff's law.

According to Blackman's theory, stated in § 1, chemical reactions in the living organism follow van 't Hoff's law, which says that the reaction-velocity increases 2 to 3 fold for each rise of temperature of 10° C.

The behaviour of the presentation-time in this respect could not be predicted theoretically. In the case of photo-tropism one could have expected van 't Hoff's law to apply, for Blaauw [1] has pointed out, that probably phototropic perception occurs through a photo-chemical reaction. With regard to geotropism however, perception by means of a chemical reaction was not to be anticipated. Only a series of exact figures could settle the question as to the application of van 't Hoff's law to the field of geotropism.

When we ask ourselves, what is the process, which is influenced by temperature and of which we determine the reaction velocity by means of the presentation-time, it is at once clear, that this process is not „reaction" as contrasted generally with perception. The length of the presentation-time will depend upon the perception or upon any other process, which makes its influence felt upon the threshold of stimulation.

The presentation-time was found to be longer when the temperature was higher; the chemical reaction-velocity must be greater when temperature is rising; therefore I have regarded the reaction-velocity of the process determining the presentation-time as inversely proportional to the presentation-time. If this process be the perception, this assumption is surely quite valid, as the presentation-time is shorter when the perception proceeds faster. The

1) A. H. Blaauw, 1909.

temperature-coefficient for a rise of 10° C. (Q_{10}) is thus found in this case by taking the relation $\frac{K_{20}}{K_{30}}$, $\frac{K_{10}}{K_{20}}$ etc., instead of $\frac{K_{30}}{K_{20}}$, $\frac{K_{20}}{K_{10}}$ etc.

Thus from the values of the presentation-time at different temperatures found in this investigation we calculate the following values of the temperature-coefficient Q_{10} (cf. the table in § 9):

$$\frac{K^0}{K_{10}} = \frac{72'}{10'40''} = 6.8, \quad \frac{K_5}{K_{15}} = \frac{16'}{6'} = 2.6, \quad \frac{K_{10}}{K_{20}} = \frac{10'40''}{4'20''} = 2.5,$$

$$\frac{K_{15}}{K_{25}} = \frac{6'}{2'20'} = 2.6, \quad \frac{K_{20}}{K_{30}} = \frac{4'20''}{1'40'} = 2.6, \quad \frac{K_{25}}{K_{35}} = \frac{2'20''}{2'30''} = 0.93,$$

$$\frac{K_{30}}{K_{40}} = \frac{1'40''}{260'} = 0.0064.$$

From these figures it is clear, that between 5° C. and 30° C. van 't Hoff's law applies to the geotropic presentation-time. The temperature-coefficient Q_{10} is 2.6.

At 0° C. the presentation-time is a good deal longer then it should be according to van 't Hoff's law [1]; probably this fact is connected with the cessation of growth at that temperature.

Above 30° C. the harmful influence of higher temperatures makes itself felt, so that there too the temperature-coefficient does not follow van 't Hoff's law.

Speaking generally we can say that the process, of which the reaction-velocity is inversely proportional to the presentation-time, follows van 't Hoff's law. For

1) Dr. Kanitz pointed out in a letter, that this sudden change in the temperature-coefficient at 0° C. becomes much more striking when calculating Q_{10} with the aid of the formula $Q_{10} = 10 \frac{10 (\log K_0 - \log K_5)}{5-0}$. We find in this way $Q_{10} = 20.3$.

convenience sake we say the presentation-time follows this law. If we ask what conclusions can be drawn from this fact regarding the nature of the perception-process, we have to acknowledge that it does not allow of any certain conclusions being drawn.

The only conclusion we can draw is that the presentation-time in respect of temperature depends upon a chemical process, which follows van 't Hoff's law; that this process is identical with the perception by no means follows.

Discussing further the nature of this process we have before us several possibilities, among which we can make no choice. One could think perception itself to be this process, so that perception would take place by means of gravity directly influencing a chemical reaction, but I cannot conceive how this could take place, nor do I think it very probable. Secondly we could take our starting-point in the statolith-theory. I do not say I think the statolith-theory to be right, my only object is to show that these facts can also find an explanation by this line of thought. Then our argument runs as follows: Perception needs starch-grains and the stimulus will be greater when the number of starch-grains is greater, if we suppose stimulation to be proportional to the number of starch-grains. Formation and solution of starch-grains are chemical processes, and it may be possible that the formation of starch-grains increases with a rise of temperature, and does so according to van 't Hoff's law. At very high temperatures on the contrary the solution of starch-grains should increase rapidly. The observations of Haberlandt at low, and of Francis Darwin at high temperatures, mentioned in § 2, could also be explained very readily in this way.

Thirdly we could imagine enzymes coming into play.

In this case the action of the enzyme might be the process in question, or the formation of the enzyme, as the perception would proceed faster if the quantity of the enzyme were greater.

These considerations are only given here to point out clearly that geotropic perception is not necessarily a simple chemical process, but merely that van 't Hoff's law is applicable to the presentation-time; this one fact alone does not make it possible to draw conclusions about the nature of perception.

In summarising we can say that with respect to van 't Hoff's law Blackman's theory is confirmed by this investigation. Just as Miss Matthaei found in the case of assimilation, and Kuyper in the case of respiration, so here too the reaction-velocity at average temperatures increases at the same rate for every 10° C. rise of temperature. The temperature-coefficient is 2.6.

The paper by van Iterson and Miss van Amstel, who concluded from their experiments that Blackman's theory must be rejected, will be discussed separately in § 15.

§ 13. Optimum and time-factor.

One of the cardinal points in Blackman's paper is the theory that the optimum is not the expression of a primary general relation between temperature and a physiological process, but varies with the time of observation. Closely connected with this is the fact (supposed to be of much importance by Blackman), that at higher and harmful temperatures the intensity of a physiological process decreases in subsequent hours, which falling off is strongest in the first hours of a stay, at a given high temperature. I recall the way in which Blackman thought it possible to reach the theoretical initial value

at a definite high temperatuse, viz. by extrapolation from
the time-curves, which represent the intensity of the
process after 1, 2, 3 and more hours; by this extrapolation
the value after a time zero should be obtained (cf. § 1).

In this section we will trace how far Blackman's
views upon the subject are confirmed by the results of
this investigation. To this end we enquire in the first
place whether the harmful influence of higher temperatures
has made itself felt as a time-function or not. The results
at 30° C. we disregard for the present.

The time-curves in the case of 35° C. and 37° C. (plate
III and V) are indeed comparable with Blackman's
diagram as rendered in fig. 1. Of course it must be kept
in view that Blackman's curves descend and here the
curves ascend (cf. what was said in § 12). The figures of
importance in this respect are the values found between
35° C. and 39° C., therefore I reprint them here (cf. the
table in § 9).

Temperature.	1 hours' preliminary warming.	2 hours' preliminary warming.	4 hours' preliminary warming.	6 hours' preliminary warming.	12 hours' preliminary warming.	24 hours' preliminary warming.
35°	2′30″	3′30″	4′	4′	5′	5′
37°	9′20″	16′	—	21′40″	—	21′40″
38°	11′30″	19′10″	38′	53′	75′	347′
39°	23′	40′	—	—	—	—

This table does not at all show a regular increase of
the presentation-time which could be represented by

means of a logarithmic curve. At 35° C. the increase of
the presentation-time is very rapid in the first hour; much
less rapid after more hours preliminary warming; so that
after 12 hours the curve (Plate III, fig. 2) becomes hori-
zontal. At 38° C. on the contrary the increase during the
subsequent hours is nearly the same, even more in the
second than in the first 12 hours. Moreover the figures
show too much irregularity as to make it possible to
extrapolate to a time zero. When trying to do so at 35° C.
we arrive at a value nearly half as high as the value
calculated with the aid of Van 't Hoff's law. At 37° C.
the value obtained by this extrapolation is even negative.

Hence we find, that the harmful influence of high
temperatures is indeed a time-function, and that this
influence makes itself especially felt at the commencement.
Thus extrapolation as used by Blackman does not
apply to our case.

Now the question arises, whether on account of these
results Blackman's theory has to be rejected or not. Is
there any reason, why this extrapolation was possible in
the case of assimilation (Miss Matthaei) and is not
applicable here?

We can answer this question when taking into account
the fact that the favourable influence of high temperatures
also needs time to make itself felt. Thus this favourable
influence, which causes a shortening of the presentation-time,
is also a function of the time of preliminary warming.

I consider the values found at 30° C. to be the strongest
argument in favour of this opinion; we found there
(cf. the table in § 9):

	1 hour	2 hours	4 hours	6 hours	12 hours	24 hours.
30° C.	3'30"	2'30"	2'10"	1'50"	1'40"	1'40"

Only after 12 hour's preliminary warming the value is
reached which would be expected according to van 't

Hoff's law. It appears very clearly from these figures, that the favourable influence of the temperature of 30° C. is seen only after a long preliminary warming.

The temperature of 30° C. has already a harmful influence too, as is shown by the above figures and more clearly by the curves on plate V. After one hours' warming the presentation-time at 30° C. is 3′30″ and in the next hour it decreases to 2′30″. Now this value 3′30″ after 1 hour cannot be explained if we do not take into account a harmful influence, which at first hindered the presentation-time from becoming lower. It could have been lower after 1 hour, for at 25° C. (at which no harmful influence can be traced) the value after 1 hour is only 2′20″.

Summarising we find at 30° C. first a harmful influence of little importance, and further a favourable influence, which is a function of the time of preliminary warming, and overcomes the harmful influence, so as to make the presentation-time reach the theoretical value according to van 't Hoff's law.

It is not only on the ground of my own results obtained at 30° C. that I offer the opinion, that the favourable influence of a high temperature needs some time to make itself fully felt; in various places in the literature on this subject the same idea is to be found, and several facts find an easy explanation in this way.

As early as 1860 Sachs [1] wrote: „Jede Temperatur wirkt auf die Vegetationsprocesse, ob sie in der Zeit der Keimung oder später fallen, nur dann, wenn sie eine bestimmte Zeit hindurch anhält". An instance is to be found in Sachs' paper on the influence of temperature on growth. [2] On plates III and IV temperature-curves are

1) J. Sachs, 1860, p. 358.
2) J. Sachs, 1872.

represented and under them the corresponding growth-
curves. The inversion-points of the growth-curves lie on
the average one hour later than those of the temperature-
curves; which proves, that during the first hour of rising
temperature growth proceeded still under the influence of
the preceeding fall of temperature.

The investigators who occupied themselves with Black-
man's theory afford us further instances. Miss Matthaei [1]
after heating the experimental leaves up to the desired
temperature had to wait one hour and a half before she
could start her experiments. Blackman [2] mentioning
this fact adds: „Hardly any investigators have allowed a
shorter preliminary time." Van Iterson and Miss
van Amstel [3] investigating the alcoholic fermentation
had to wait until 25 to 30 cc. gas had escaped, before
the gas-production (at temperatures which were not harmful)
became sufficiently regular.

. My best argument I find in Kuyper's investigation.
Kuyper [4] had to wait about one hour at 25° C. and at
30° C. before he could make his first observation of the
respiration, because otherwise the CO_2 production was
very small. · He adds and I emphasize these words:
„evidently· the CO_2-production is not at once at the height
corresponding with the degree of warming." And discus-
sing his results Kuyper says a propos of his results
between 30° C. and 40° C. [5]: „In my opinion we have
here two processes combined, which together are the
causes of the CO_2-production in normal respiration. One

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1) G. L. C. Matthaei, 1905, p. 62.
2) F. F. Blackman, 1905, p. 286.
3) G. van Iterson Jr. and Miss J. van Amstel, 1910, p. 109.
4) J. Kuyper, 1910, p. 170.
5) J. Kuyper, 1910, p. 206.

is inhibited at high temperature, almost immediately and very greatly, the other is stimulated rather slowly during the stay at the high temperature". Apparently Kuyper also distinguishes a favourable and a harmful influence of high temperatures, which two influences make themselves felt at a different rate.

These quotations sufficiently prove the hypothesis, that the favourable influence of high temperatures requires time to make itself fully felt. On the other hand several exceptions to Blackman's theory may be easily explained in this way. Blackman starts from the supposition, that the intensity of a physiological process after a rise of temperature immediately assumes the value corresponding to that temperature, and afterwards (if the temperature in question is a harmful one) only gradually undergoes the harmful influence. As stated above, it has been seen again and again, that the reaction-velocity corresponding to a given high temperature is not obtained immediately. This explains, why in most cases extrapolation from the time-curves to a time zero does not give the values to be expected according to van 't Hoff's law. These theoretical values after a time zero do not exist in reality, as we shall now demonstrate.

When no harmful influence was at work the value corresponding to a given high temperature (calculated according to van 't Hoff's law) would indeed be reached after some time, but now the harmful influence of the high temperature has already caused a fall in the intensity of the process before this high value is actually reached. From the beginning the values are lower than would be expected according to Blackman's theory.

For this reason also it will be impossible to find the theoretical value after a time zero by extrapolation from

the curve through the values found experimentally after
1, 2 and more hours preliminary heating.

Not only at harmful temperatures (above the optimum),
but even at those temperatures which are not directly
harmful, this phenomenon can give rise to errors. In this
case also it is possible, that after one or two hours the
reaction-velocity is not yet at its full height. In a given
case everything depends upon the relative rapidity of the
two opposing influences. If the favourable influence has
its full effect almost instantaneously, while the harmful
influence on the contrary makes itself felt only gradually,
we shall find a state of things similar to the case of
assimilation, investigated by Miss Matthaei. If on the
other hand both influences work slowly, we get curves,
as have been found by Kuyper in the case of respiration,
and by my self in the case of the geotropic presentation-
time. At very high temperatures the harmful influence
is predominant, and the initial values are considerably
lower than they should be, — were it possible to get the
theoretical values after a time zero by extrapolation. At
slightly lower temperatures we see first the harmful in-
fluence and afterwards during a short time a favourable
influence, as Kuyper found at some temperatures, or
the favourable influence lasts a long time after a short
preliminary harmful influence, as was the case in my
experiments at 30° C. When both influences are at work
with the same intensity and at the same rate it may be
possible to get curves which are nearly horizontal.

Hitherto I have not discussed the question, whether
the optimum varies with the time of observation. The
curves in Fig. 6, p. 58 answer this 'question. The presen-
tation-time after one hours' preliminary warming has
there been indicated by means of a thick line. This line

does not show a marked optimum, but it is like the curve found by Czapek. The lowest value is 2'20" at 25° C., but at 30° C. we find 3'30" and at 35° C. 2'30". The optimum here lies at 25° C. When tracing the thin line, running through the points representing the presentation-time after 12 hours' preliminary warming, we find a marked optimum at 30° C.; the values just mentioned are in that case: 2'20", 1'40", 5'. This slight displacement was the only variability of the optimum that could be obtained.

Summarising we see that the time-factor makes itself felt very markedly, not only with regard to the harmful influence, but also as regards the favourable influence of the high temperatures. The variability of the optimum with the time of observation is only very small.

§ 14. Limiting factors.

I briefly repeat here what was said in § 1 about Blackman's views on limiting factors. When tracing the influence of some factor upon a physiological process, which process increases as to its intensity when that factor is increasing, we arrive at a point, where a further increase of the factor mentioned does not give rise to a further increase of the intensity of the process, because some other factor in the process puts a limit to further increase. In § 1 the assimilation in its relation to the amount of CO_2 available was quoted as an instance (cf. fig. 2 on p. 6). When the amount of CO_2 is increasing, assimilation will also increase, until a point is reached, where the amount of radiant energy available (when we suppose this factor to remain constant during the experiments) will allow no greater assimilation. From that point

assimilation will remain constant, even when the amount of CO_2 is increasing further. Apparently assimilation is from this point onwards independent of the amount of available CO_2 — in reality the amount of available radiant energy acts as limiting factor.

In the same way a great many conditions can act as limiting factors in physiological experiments; and the fact, that conditions are kept constant makes it all the more probable that they will act in this way. It is obvious, that this fact has to be kept in view, else erroneous conclusions will be drawn quite easily. Thus for instance in the above mentioned case the conclusion is obvious (and it has been arrived at by several investigators) that above a certain limit a further increase of the amount of CO_2 available is of no further influence upon the assimilation, while in reality this influence certainly exists, but cannot be seen because of the amount of available radiant energy acting as the limiting factor.

We will now try to examine, whether in the present investigation limiting factors have played a part. Generally speaking a limiting factor will be present, when a rising or falling curve quite suddenly becomes horizontal (cf. fig. 2 on p. 6).

When we look at the thick line in Fig. 6 and 7, p. 58 and 60 (representing the presentation-time after one hours' preliminary warming), we see a more or less horizontal part between 25° C. and 35° C. Here a limiting factor might perhaps be supposed to occur. This being the case there must be a factor at 30° C., which loses its limiting powers after a longer stay at this temperature, i. e. changes in such a way that it no longer counteracts a greater intensity of the process.

I do not know what this factor might be; perhaps we could imagine of a larger amount of an enzyme being

required at this temperature, and this larger amount being formed only slowly during the stay at this temperature.

The results of Czapek, represented by a descending line, which from 15° C. to 30° C. runs horizontally, also give rise to the supposition, that here a limiting factor came into play.

A second point, where the curve probably does not accurately represent the relation between temperature and presentation-time, is at 0° C., at which temperature the presentation-time suddenly becomes extraordinary long. The temperature-coefficient between 15° C. and 5° C. is 2.6, between 5° C. and 0° C. it is 20.3 (cf. p. 67). I think it very probable that the cause of this phenomenon must be sought in the fact that at this temperature growth is nearly at a standstill. If the sudden rise in the presentation-time is really dependent on this fact, we have here another instance of a secondary influence and might range this under the limiting factors in Blackman's sense. Our knowledge of this subject is, however, not sufficient, to say anything positively. The lack of an exhaustive investigation of the relation between temperature and growth makes itself felt here.

§ 15. The investigation of van Iterson and Miss van Amstel.

So far this investigation is the only one in which the authors have opposed Blackman's theory. We must therefore consider more fully, whether the results obtained there really justify the conclusion that Blackman's theory must be rejected. [1]

1) I give a very short summary only; for all details the original paper must be consulted.

Van Iterson and Miss van Amstel investigated the influence of temperature on alcoholic fermentation and on the inversion of cane-sugar [1]).

The reaction-velocity of alcoholic fermentation was measured by means of the amount of CO_2 (calculated in cc.) produced per second. The yeast was mixed with a certain amount of water and warmed beforehand apart from the sugar-solution. When both solutions had arrived at the temperature of the bath they were mixed. After the production of 25 to 30 cc. gas the further production was sufficiently regular to start the observations. The total amount of gas collected did not exceed 100 cc. and determinations were made of the time needed for the production of the subsequent volumes of 2, 5, 10 or 25 cc. CO_2, the amount of each being regulated according to the intensity of the gas-production.

The reaction-velocity of alcoholic fermentation proved to be independent of the time of preliminary warming up to 45° C., if this time did not exceed 20 minutes. Above 45° C. the influence of the time of preliminary warming appeared, and the reaction-velocity diminished during the experiment.

The reaction-velocities found in this way have been collected in the following table:

1) Both processes yielded the same result; as only the first one has been described more fully, I deal with this alone.

Tempera- ture in degrees C.	Velocity after 5 min. pre- liminary warming.	Velocity after 10 min. pre- liminary warming.	Velocity after 15 min. pre- liminary warming.	Velocity after 20 min. pre- liminary warming.
20°	—	—	—	0.087
25°	—	—	—	0.139
30°	—	—	—	0.199
33°	—	—	—	0.239
36°	—	—	—	0.298
39°	—	—	—	0.360
42°	—	—	—	0.385
45°	—	—	—	0.405
46°	0.41^5	0.39^5	0.37	0.34
47°	0.42^5	0.38	0.33^5	0.30^5
48°	0.40	0.36	0.30^5	0.27
50°	0.40	0.23^5	0.20^5	0.17^5
52°	0.29^5	0.13^5	0.10	0.06^5
53°	0.16^5	0.10^5	0.05^5	0.02
54°	0.12	0.04	0.01^5	—
55°	0.06	—	—	—
56°	0.02	—	—	—
57°	0.00	—	—	—

In this table we see the position of the optimum dependent on the time of preliminary warming.

Testing van 't Hoff's law on the values found at the temperatures under 45° C. the writers find the temperature-coefficient:

$$\frac{V_{30}}{V_{20}} = 2.3, \quad \frac{V_{35}}{V_{25}} = 2.0, \quad \frac{V_{40}}{V_{30}} = 1.8, \quad \frac{V_{45}}{V_{35}} = 1.5.$$

Their conclusion from these figures is: „The value of the quotient appears to be considerably less at high tem-

perature than it was at lower temperature; only at the last mentioned ones it reaches the value to be expected according to van 't Hoff's law.

Van Iterson points aut, that, according to Blackman, this decrease of the temperature-coefficient must be ascribed to a harmful influence, but that during the warming-times used here such an influence had not been seen and he adds: „It must therefore be pointed out very emphatically, that already on account of the course of the optimum-curve below harmful temperatures the theory of Duclaux and Blackman must be rejected".

As regards the values found at harmful temperatures, i. e. above 45° C., van Iterson also arrives at the conclusion that they do not confirm Blackman's theory. The values of the reaction-velocity found after a time zero show a distinct optimum, no matter in which way they are determined. The time-curves show only a slight falling off during the first few minutes, which is by no means sufficient to give on extrapolation the values according to van 't Hoff's law.

Summarising van Iterson mentions as his principal results, that the curve corresponding to a preliminary warming-time of 0 minutes is a pronounced optimum-curve; and secondly that considerable deviations from van 't Hoff's law appear long before the harmful temperatures are reached; for these two reasons he thinks Blackman's theory must be rejected.

When trying to answer van Iterson's objections we must make clear at the outset, to what extent van 't Hoff's law holds good in the field of chemistry. In doing so, we see that there too the same decrease of the temperature-coefficient is to be observed. Thus Plotnikow [1]

1) J. Plotnikow, 1905, p. 632.

found the temperature-coefficient 6.2 for the reaction
between ethylene and bromine ad —78° C. Trautz and
Volkman, [1]) for the saponification of ethyl-acetate by
baryta, give the following values for the temperature-
coefficient:

$$\frac{10^o}{0^o} = 1.96, \quad \frac{20^o}{10^o} = 2.04, \quad \frac{30^o}{20^o} = 1.90, \quad \frac{40^o}{30^o} = 1.75,$$

$$\frac{50^o}{40^o} = 1.60, \quad \frac{60^o}{50^o} = 1.45.$$

For the saponification of propyl-acetate the corresponding
values: 1.63, 2.00, 1.81, 1.70, 1.55, 1.43.

Cohen [2]) also points out that the temperature-coefficient
in a chemical reaction is in general liable to vary with
change of temperature. At high temperatures the tem-
perature-coefficient decreases, at low ones it rises.

The other reason why van Iterson believes Black-
man's theory to be untenable, is that the curve which
represents the connection between alcoholic fermentation
and temperature, is also a pronounced optimum-curve for
a preliminary warming-time of 0 minutes. In my opinion
the authors have attached too great weight to this
objection also. Various points can be brought forward to
explain this phenomenon.

In the first place, there is the fact already mentioned,
that the temperature-coefficient decreases with a rise of
temperature.

Further it must be pointed out that van 't Hoff's law
applies less strictly in the field of botany than in that
of chemistry, for the living organism may not be regarded
simply as a homogeneous system, and it is only to such

1) M. Trautz and K. Th. Volkman, 1908, p. 68 and 78.
2) E. Cohen, 1907, p. 39.

a system that van 't Hoff's law can be applied with accuracy..

Moreover even in this case a special factor comes into play, through which an important deviation at higher temperatures is a priori probable. The reaction here takes place between the zymase which is enclosed within the living cell and the sugar-solution outside it. Thus the transformation only takes place when the sugar diffuses inwards and the reaction-products diffuse outwards in the opposite direction. Now, since at each 10° C. rise of temperature the velocity of diffusion only rises about 20 % [1]) and the velocity of fermentation 150—200 %, it is to be expected that at higher temperatures the velocity of fermentation will remain considerably under the theoretical values, in consequence of the diffusion not proceeding quickly enough.

Finally, the possibility must be considered that also in alcoholic fermentation the favourable influence of higher temperatures first makes itself felt as a function of time, in the same way as was the case in this inquiry at 30° C., and that the theoretical values according to van 't Hoff's law have here too no real existence. For if it takes a certain time for the reaction-velocity to reach the value belonging to that temperature then this value will never be reached, because, before that happens the harmful influence of the high temperature will already have made its action felt. The values obtained for the reaction-velocity at high temperatures will then, especially after a short time of previous warming, be lower than ought to be the case according to Blackman's theory. The values when extrapolated for time 0 will also be found too low.

1) cf. Cohen, 1907, p. 126.

Summarising we see, that some. of van Iterson's objections to Blackman's theory are not so serious as he thought them to be, while on the other hand several reasons can be adduced in explanation for the deviations found in his investigation.

As only van Iterson's results stand against Blackman's theory and all other processes so far investigated, more or less agree with it, I do not think it advisable to reject Blackman's theory.

Since the publication of the foregoing considerations a second paper of van Iterson and Miss van Amstel [1]) has appeared, in which the conclusion that Blackman's theory has to be rejected is defended against my objections.

I advanced three arguments, why I thought this conclusion not justified by the authors' results. The three reasons, which might be the cause that Blackman's theory was not applicable to the results obtained in the cases of sugar-inversion and alcoholic fermentation were:

1°. The living organism is no homogeneous system.
2°. Even in vitro van 't Hoff's law has only approximate value in some cases.
3°. Since in many cases in plant-physiology the favourable influence of higher temperatures does not make itself felt at once, perhaps here too such a time-factor may play a part.

In answering these three points, van Iterson begins with the last one; and the greater part of his paper bears on the discussion of this point. Now I want to emphasize that this point has had a very subordinate place in my argument; I only said: „finally the possibility is not excluded, that the favourable influence of high

1) G. van Iterson Jr. and Miss J. van Amstel. II. 1910.

temperatures, which makes itself only gradually felt during the preliminary warming-time and was spoken of in § 13, also plays a part here [1]).

After the figures published by the authors I readily accept their statement, that this is not the case [2]).

The objections stated under 1° and 2° are more important in my opinion, and on these points I am not convinced by van Iterson's refutation. It may be, that diffusion acts not as a limiting factor, but surely there is more than diffusion only, which constitutes a difference between the reactions in question and a homogeneous system.

Van Iterson does not think the fact mentioned under 2° to be in support of Blackman's theory: for „what is the use of Blackman's theory, if physiological processes are allowed to divert from van 't Hoff's law even at temperatures which are not harmful?"

This last question brings me to the cardinal point of this discussion.

Blackman's theory started from the idea that van 't Hoff's law, which holds good for so many chemical reactions, should be applicable to chemical reactions in the living organism also. Van Iterson and Miss van Amstel put this theory to a practical test in the cases of alcoholic fermentation and inversion of cane-sugar, and have found it inapplicable. Now they conclude that Blackman's theory is to be rejected, and they say so quite generally. This conclusion I did not think justified by the facts and I still hold this opinion. Blackman's

1) Of course I maintain my opinion, that the favourable influence of high temperatures needs some time to make its influence fully felt. The facts quoted in § 13 are there to prove it. The case of growth quoted from Sachs is especially convincing.

theory itself, by the way in which it was deduced, gives rise to the supposition, that it will not prove applicable to all cases. The theoretical reasons for which this could be anticipated are the facts mentioned above under 1º and 2º. In the case of purely chemical reactions van 't Hoff's law does not always give the expression of the change of the reaction-velocity (and van Iterson adds some very good instances of this fact), and in the second place, the living organism differs widely from a homogeneous system.

These exceptions are by no means sufficient to make Blackman's theory worthless. Nor is the fact, that two cases are found, to which Blackman's theory does not apply, sufficient to conclude that this theory has to be rejected. The less so, as in all other processes hitherto investigated, it has proved to be a valuable means of reaching a better understanding of the origin of the optimum-curve.

§ 16. Summary of results.

Summarising this investigation we can say, that Blackman's theory is applicable to the influence of temperature on the presentation-time in geotropism in the case of coleoptiles of *Avena sativa*, provided that the favourable influence of high temperatures as a time-function is taken into account.

Van 't Hoff's law holds good in the case here investigated between 5º C. and 30º C.; the coefficient for 10º C. rise of temperature is 2.6.

Between 0º C. and 25º C. the same presentation-time is found after 1 hours' and after several hours' preliminary warming.

At 30º C. the influence of the duration of the preliminary warming is very clearly seen. During the first hour

the harmful influence dominates, during the following hours the favourable influence makes itself felt, which influence causes no further alteration of the presentation-time when the preliminary warming is extended over 12 hours.

At 35° C. and still higher temperatures the harmful influence of the high temperature preponderates from the first hour. This harmful influence gradually becomes less during the successive hours of preliminary warming. A favourable influence as time-function cannot here be distinguished.

At 37° C. the behaviour of the presentation-time is the same as at 35° C., only the harmful influence is more powerful. At 38° C. the harmful influence is not exhausted after some hours, at least after 24 hours' warming the adverse influence does not yet show any diminution. At 39° C. and 40° C. this is even more strikingly the case.

The optimum was not variable with the time of preliminary warming to the extent one would have expected according to Blackman's theory. A slight displacement from 25° C. to 30° C. was all that could be obtained. This fact is doubtless connected with the favourable influence being a time-function.

According to Blackman extrapolation from the curves representing the intensity of the process after successive hours of warming, should give the intensity of the process after a time zero, and the values thus obtained, should harmonize with the values, calculated according to van 't Hoff's law, starting from the values found at low temperatures.

In the present case this extrapolation afforded values, differing widely from the theoretical ones. The explanation of this discrepancy must be looked for in the fact, that Blackman's theory does not take into account that the favourable influence of high temperatures is also a time-

function. When allowing for this, the results obtained do not contradict the theory that the optimum is the result of secondary influences.

Blackman's view that the optimum is not the expression of a primary, general relation between temperature and physiological processes, is confirmed by this investigation.

The way in which the presentation-time changes according to the temperature shows that we have here to do with the influence of temperature on a chemical process. Therefore we may say that perception of geotropic stimulation is connected with a chemical process.

APPENDIX. TABLES.

The following 42 tables contain a full statement of all the experiments upon which the conclusions arrived at in this paper are based.

Each table deals with one temperature and with one time of preliminary warming. Thus the first table (I A) gives the results of the experiments made at 0° C. and after 1 hours' preliminary warming. Table II A gives similar results obtained under the same conditions; the only difference is that the experiments geven in I A were not made in the thermostat but out of doors in the snow. Table II B relates to experiments made at 0° C. and 4 hours' preliminary warming. As I did not make any experiments at 0° C. with a longer preliminary warming, no further tables relating to 0° C. are given. Table III A and III B deal with the experiments at 5° C. and 1 or 4 hours' preliminary warming etc.

Buitenzorg, 1 May 1911.

TABLE I A.

0° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
885'	B 24	26-I-10	28	28	28	28	100 %	900'
180'	B 26	27-I-10	30	29	30	29	97 %	210'
90'	B 28	27-I-10	33	23	33	23	70 %	140'
75' {	B 33	28-I-10	26	13	} 56	33	59 %	135'
	B 34	29-I-10	30	20				110'
60' {	B 27	27-I-10	30	3	} 57	9	16 %	—
	B 32	28-I-10	27	6				—
45'	B 31	28-I-10	29	0	29	0	0 %	—
30'	B 22	26-I-10	26	0	26	0	0 %	—

TABLE II A.

0° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
60' {	C 277	18-VI-10	50	34	} 100	68	68 %	110'
	C 281	20-VI-10	50	34				100'
45' {	C 278	18-VI-10	50	30	} 75	39	52 %	90'
	C 282	20-VI-10	25	9				—
30' {	C 279	18-VI-10	50	12	} 75	18	24 %	—
	C 283	20-VI-10	25	6				—
25' {	C 274	17-VI-10	25	0	} 75	0	0 %	—
	C 275	17-VI-10	50	0				—
15'	C 273	17-VI-10	50	0	50	0	0 %	—

TABLE II B.

0° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
60'	C 286	20-VI-10	25	19	—	—	76 %	95'
45'	C 285	20-VI-10	40	13	—	—	33 %	—
30'	C 284	20-VI-10	25	6	—	—	24 %	—
25'	C 276	17-VI-10	50	0	—	—	0 %	—

TABLE III A.

5° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
13'	C 266	15-VI-10	50	30	—	—	60 %	60'
11'	C 265	15-VI-10	49	28	—	—	57 %	55'
9'	C 264	15-VI-10	50	23	—	—	46 %	65'

TABLE III B.

5° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
13'	C 269	15-VI-10	25	16	50	29	58 %	55'·
	*C 272	15-VI-10	25	13				70'
11'	C 268	15-VI-10	25	12	50	22	44 %	60'
	*C 271	15-VI-10	25	10				70'
9'	C 267	15-VI-10	25	9	50	18	36 %	—
	*C 270	15-VI-10	25	9				—

*) C 270—272 during the reaction-time at 5° C.

TABLE IV B.

10° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
8'	C 254	4-VI-10	16	12	61	39	64 %	45'
	C 261	13-VI-10	45	27				45'
7'	C 253	4-VI-10	20	11	70	32	46 %	45'
	C 260	13-VI-10	50	21				55'
6'	C 252	4-VI-10	23	10	68	28	41 %	50'
	C 259	13-VI-10	45	18				50'

TABLE IV A.

10° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
9'	C 255	11-VI-10	50	39	50	39	78 %	40'
8'	C 249	4-VI-10	25	14	73	46	63 %	55'
	C 256	11-VI-10	48	32				40'
7'	C 246	3-VI-10	30	15	195	87	45 %	55'
	C 250	4-IV-10	25	8				—
	C 257	11-VI-10	50	28				40'
	C 258	13-VI-10	90	36				50'
6'	C 247	3-VI-10	30	9	45	9	20 %	—
	C 251	4-VI-10	15	0				—
5'	C 248	3-VI-10	29	7	29	7	24 %	—

TABLE V A.

15° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
7′	C 203	18-V-10	33	32	49	47	96 %	35′
	C 230	27-V-10	16	15				35′
6′	C 214	20-V-10	15	12	50	36	72 %	40′
	C 220	26-V-10	10	8				45′
	C 229	27-V-10	25	16				50′
5′	C 204	18-V-10	25	20	80	56	70 %	35′
	C 219	26-V-10	14	6				55′
	C 228	27-V-10	25	17				55′
	C 233	28-V-10	16	13				45′
4′	C 213	20-V-10	15	8	52	24	46 %	35′
	C 227	27-V-10	25	11				50′
	C 232	28-V-10	12	5				50′
3′	C 212	20-V-10	15	5	30	10	33 %	—
	C 231	28-V-10	15	5				—
2′	C 211	20-V-10	15	0	15	0	0 %	—

TABLE V B.

15° Centigrade.   2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
7'	C 205	18-V-10	32	31	32	31	97 %	35'
6'	C 210	19-V-10	13	13	28	22	79 %	35'
	C 221	26-V-10	15	9				50'
5'	C 206	18-V-10	33	27	58	43	74 %	35'
	C 222	26-V-10	12	6				55'
	C 236	28-V-10	13	10				40'
4'	C 209	19-V-10	33	17	48	22	46 %	50'
	C 235	28-V-10	15	5				—
3'	C 208	19-V-10	50	18	65	21	32 %	—
	C 234	28-V-10	15	3				—
2'	C 207	19-V-10	31	0	31	0	0 %	—

TABLE V C.

15° Centigrade.   24 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
7'	C 226	27-V-10	16	16	16	16	100 %	40'
6'	C 225	27-V-10	16	16	32	31	97 %	35'
	C 240	28-V-10	16	15				40'
5'	C 224	27-V-10	17	15	42	28	67 %	40'
	C 239	28-V-10	25	13				50'
4'	C 223	27-V-10	15	7	55	25	45 %	50'
	C 238	28-V-10	40	18				45'
3'	C 237	28-V-10	15	5	15	5	33 %	—

TABLE VI A.

20° Centigrade. 1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
4'40″	C 5	25-II-10	50	41	—	—	82 %	40'
4'20″	C 4	25-II-10	50	26	—	—	52 %	55'
4'	C 6	25-II-10	50	14	—	—	28 %	—

TABLE VI B.

20° Centigrade. 8 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
5'	C 62	6-IV-10	50	44	—	—	88 %	40'
4'40″	C 63	6-IV-10	50	38	—	—	76 %	45'
4'20″	C 64	6-IV-10	50	28	—	—	56 %	50'
4'	C 65	6-IV-10	50	24	—	—	48 %	55'

Table VII A.

20° Centigradè.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
5'30"	C 237	28-V-10	30	28	30	28	93 %	30'
5'	C 242	30-V-10	25	15				50'
	C 345	3-VI-10	13	13				40'
	C 355	15-VII-10	18	15	81	68	85 %	35'
	C 263	15-VI-10	25	25				35'
4'	C 215	20-V-10	24	19				35'
	C 238	28-V-10	25	16				35'
	C 241	30-V-10	25	15	121	88	73 %	55'
	C 244	3-VI-10	17	16				40'
	C 354	15-VII-10	30	22				35'
3'	C 216	20-V-10	13	6				45'
	C 240	30-V-10	25	10				60'
	C 243	3-VI-10	16	13	101	52	51 %	40'
	C 353	15-VII-10	22	13				35'
	C 262	15-VI-10	25	10				50'
2'	C 239	30-V-10	25	5	25	5	20 %	—

T a b l e VIII A.

25° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent	Reaction-time.
4′	C 82	12-IV-10	36	36	36	36	100 %	40′
3′30″	C 83	12-IV-10	25	23	25	23	92 %	40′
	C 84	12-IV-10	40	26				40′
3′	C 373	12-VIII-10	17	10	74	45	60 %	45′
	*C 374	12-VIII-10	17	9				50′
2′30″	C 85	12-IV-10	45	26	45	26	55 %	40′
	C 95	14-IV-10	25	12				45′
2′	C 371	12-VIII-10	15	6	55	24	44 %	45′
	*C 372	12-VIII-10	15	6				45′
1′30″	C 96	14-IV-10	25	5	25	5	20 %	—
1′	C 97	14-IV-10	25	0	25	0	0 %	—

* C 372 and 374 during the reaction-time at 25° C.

TABLE VIII B.

25° Centigrade.   2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3'30" {	C 75	9-IV-10	50	38	} 75	62	83 %	40'
	C 98	14-IV-10	25	24				35'
3'	C 76	9-IV-10	25	20	25	20	80 %	35'
2'30"	C 77	9-IV-10	25	14	25	14	56 %	45'
2'	C 86	13-IV-10	25	6	25	6	24 %	—
1'30"	C 87	13-IV-10	25	4	25	4	16 %	—
1'	C 99	14-IV-10	25	0	25	0	0 %	—

TABLE VIII C.

25° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3'30" {	C 69	8-IV-10	25	19	} 50	43	86 %	35'
	C 100	14-IV-10	25	24				35'
3'	C 70	8-IV-10	25	16	25	16	64 %	40'
2'30"	C 71	8-IV-10	25	15	25	15	60 %	45'
2'	C 88	13-IV-10	25	5	25	5	20 %	—
1'30"	C 89	13-IV-10	25	4	25	4	16 %	—
1'	C 90	13-IV-10	25	0	25	0	0 %	—

TABLE VIII D.

25° Centigrade.　　　　　　　　6 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3'30"	C 68	7-IV-10	50	50	50	50	100 %	40'
3'	C 72	8-IV-10	25	21	25	21	84 %	40'
2'30" {	C 73	8-IV-10	25	10	} 50	30	60 %	40'
	C 78	9-IV-10	25	20				35'
2' {	C 74	8-IV-10	20	3	} 45	16	34 %	—
	C 79	9-IV-10	25	13				45'
1'30"	C 80	9-IV-10	25	14	25	14	56 %	40'
1'	C 81	9-IV-10	24	6	24	6	25 %	—

TABLE IX A.

30° Centigrade.　　　　　　　　1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
4'30" {	B 39	4-II-10	32	30	} 61	58	95 %	30'
	B 40	4-II-10	29	28				35'
4'	C 14	4-III-10	50	36	50	36	72 %	50'
3'30" {	B 41	4-II-10	32	13	} 62	31	50 %	60'
	B 42	4-II-10	30	18				60'
3' {	B 43	4-II-10	32	3	} 57	17	30 %	—
	C 43	21-III-10	25	14				55'
2'30"	C 51	24-III-10	49	21	49	21	43 %	55'
2'	C 39	19-III-10	45	0	45	0	0 %	—

TABLE IX B.

30° Centigrade.   2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
4′	C 53	24-III-10	40	38	40	38	95 %	40′
3′30″	C 26	12-III-10	50	41	50	41	82 %	35′
3′	C 29	14-III-10	50	12	145	57	40 %	—
	C 44	21-III-10	45	21				65′
	C 52	24-III-10	50	24				60′
2′30″	C 32	16-III-10	50	16	50	16	32 %	—
2′	C 40	19-III-10	50	0	50	0	0 %	—

TABLE IX C.

30° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3′30″	C 25	11-III-10	60	60	—	—	100 %	35′
3′	C 30	14-III-10	50	41	—	—	82 %	45′
2′30″	C 33	16-III-10	50	37	—	—	74 %	45′
2′	C 41	19-III-10	50	22	—	—	44 %	55′
1′30″	C 45	21-III-10	40	12	—	—	30 %	—
1′	C 46	21-III-10	45	0	—	—	0 %	—

TABLE IX D.

30° Centigrade.   6 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3′30″	C 27	12-III-10	50	48	50	48	96 %	40′
3′	C 31	14-III-10	48	38	48	38	80 %	40′
2′30″	C 34	16-III-10	50	34	50	34	68 %	50′
2′	C 42	19-III-10	46	26	46	26	57 %	55′
1′30″	C 369	10-VIII-10	15	5	31	10	32 %	—
	*C 370	10-VIII-10	16	5				—

* C 370 during the reaction-time at 30° C.

TABLE IX F.

30° Centigrade.   24 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3′	C 58	26-III-10	40	38	—	—	95 %	40′
2′	C 59	26-III-10	45	24	—	—	51 %	60′
1′30″	C 60	26-III-10	40	19	—	—	47 %	60′
1′	C 61	26-III-10	45	12	—	—	26 %	—

TABLE IX E.

30° Centigrade.   12 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
3'30"	C 38	19-III-10	50	47	50	47	94 %	35'
	C 36	17-III-10	50	33				45'
3'	C 47	23-III-10	50	30	150	99	66 %	50'
	C 54	25-III-10	50	36				45'
	C 35	16-III-10	50	39				50'
2'30"	C 55	25-III-10	50	46	100	85	85 %	35'
	C 48	23-III-10	50	44				35'
2'	C 56	25-III-10	50	28	100	72	72 %	55'
	C 49	23-III-10	50	30				50'
1'30"	C 57	23-III-10	40	8	90	38	42 %	—
1'	C 50	23-III-10	40	0	40	0	0 %	—

TABLE X A.

35° Centigrade. 1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
5′30″	C 109	18-IV-10	40	40	40	40	100 %	30′
5′	C 110	18-IV-10	40	40	40	40	100 %	35′
4′30″	C 132	23-IV-10	20	17	20	17	85 %	40′
4′	C 126	22-IV-10	25	19	50	31	62 %	35′
	C 102	15-IV-10	25	12				50′
3′30″	C 133	23-IV-10	20	14	70	58	83 %	45′
	C 111	18-IV-10	25	24				35′
	C 142	25-IV-10	25	20				40′
3′	C 127	22-IV-10	25	15	25	15	60 %	40′
2′30″	C 128	22-IV-10	20	9	65	35	54 %	55′
	C 134	23-IV-10	20	10				50′
	C 141	25-IV-10	25	16				45′
2′	C 140	25-IV-10	25	6	25	6	24 %	—
1′30″	C 139	25-IV-10	25	3	25	3	12 %	—
1′	C 147	27-IV-10	20	0	20	0	0 %	—

TABLE X B.

35° Centigrade. 2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
5'30"	C 135	23-IV-10	20	19	20	19	95 %	35'
5'	C 131	22-IV-10	20	16	20	16	80 %	40'
4'30"	C 136	23-IV-10	20	13	20	13	65 %	50'
4'	C 130	22-IV-10	20	9	93	49	53 %	50'
	C 148	27-IV-10	23	5				—
	C 156	29-IV-10	50	35				45'
3'30"	C 137	23-IV-10	20	12	70	34	49 %	50'
	C 143	25-IV-10	25	11				55'
	C 157	29-IV-10	25	11				60'
3'	C 129	22-IV-10	20	8	43	12	28 %	40'
	C 158	29-IV-10	23	4				—
2'30"	C 138	23-IV-10	18	7	43	16	37 %	—
	C 144	25-IV-10	25	9				—
2'	C 145	25-IV-10	20	5	45	10	22 %	—
	C 149	27-IV-10	25	5				—
1'30"	C 146	25-IV-10	20	2	42	2	5 %	—
	C 150	27-IV-10	22	0				—

TABLE X C.

35° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
6'	C 103	15-IV-10	25	20	42	37	90 %	35'
	C 123	21-IV-10	17	17				35'
5'30"	C 112	18-IV-10	25	19	25	19	76 %	40'
5'	C 113	18-IV-10	25	16	37	27	74 %	45'
	C 192	13-V-10	12	11				35'
4'30"	C 114	18-IV-10	25	17	43	29	67 %	45'
	C 115	20-IV-10	18	12				45
4'	C 104	15-IV-10	25	8	118	58	50 %	—
	C 116	20-IV-10	32	18				45'
	C 187	12-V-10	23	13				50'
	C 189	13-V-10	38	19				55'
3'30"	C 117	20-IV-10	18	8	38	11	29 %	50'
	C 124	21-IV-10	20	3				—
3'	C 118	20-IV-10	18	2	29	5	17 %	—
	C 191	13-V-10	11	3				—
2'30"	C 125	21-IV-10	19 -	0	41	3	7 %	—
	C 188	12-V-10	22	3				—
2'	C 190	13-V-10	10	1	10	1	10 %	—

TABLE X D.

35° Centigrade.   6 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
6'	C 162	2-V-10	16	16	16	16	100 %	35'
5'	C 160	2-V-10	38	36				35'
	C 169	4-V-10	25	22	83	69	83 %	40'
	C 185	11-V-10	20	11				55'
4'	C 161	2-V-10	20	10				55'
	C 168	4-V-10	20	14				45'
	C 183	9-V-10	25	12	101	51	50 %	60'
	C 184	11-V-10	36	15				50'
3'	C 159	2-V-10	33	11				—
	C 167	4-V-10	24	10	97	30	31 %	60'
	C 182	9-V-10	40	9				—
2'	C 166	4-V-10	24	3				—
	C 181	9-V-10	25	5	63	9	14 %	—
	C 186	11-V-10	14	1				—

TABLE X E.

35° Centigrade.   18 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
10'	C 107	16-IV-10	25	25	25	25	100 %	35'
7'	C 174	7-V-10	12	12	32	32	100 %	35'
	C 119	21-IV-10	20	20				40'
6'	C 105	16-IV-10	25	7	81	53	65 %	—
	C 120	21-IV-10	20	13				45'
	C 175	7-V-10	36	33				40'
5'	C 108	16-IV-10	25	10	60	32	53 %	45'
	C 121	21-IV-10	20	10				50'
	C 176	7-V-10	15	12				50'
4'	C 106	16-IV-10	25	7	25	7	28 %	—
3'	C 122	21-IV-10	18	0	32	6	19 %	—
	C 177	7-V-10	14	6				65'

TABLE X F.

35° Centigrade.   24 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
7'	C 164	4-V-10	20	18	20	18	90 %	45'
6'	C 151	28-IV-10	25	15	25	15	60 %	60'
	C 152	28-IV-10	20	8				70'
5'	C 165	4-V-10	18	7	63	30	48 %	50'
	C 195	14-V-10	25	15				50'
4'	C 153	28-IV-10	20	6	20	6	30 %	—
	C 154	28-IV-10	20	6				—
3'	C 163	4-V-10	24	3	64	19	30 %	—
	C 196	14-V-10	20	10				60'

TABLE X G.

35° Centigrade.   48 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
7'	C 173	6-V-10	19	15	54	48	89 %	55'
	C 200	16-V-10	35	33				45'
6'	C 172	6-V-10	20	13	20	13	65 %	60'
	C 171	6-V-10	24	5				—
5'	C 193	14-V-10	16	10	60	27	45 %	55'
	C 202	16-V-10	20	12				55'
	C 170	6-V-10	19	2				—
4'	C 194	14-V-10	10	4	46	14	30 %	50'
	C 201	16-V-10	17	8				60'

TABLE XI A.

37° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
30'	C 302	25-VI-10	32	32	32	32	100 %	40'
10'	C 301	25-VI-10	29	23	29	23	80 %	50'
9'	C 304	25-VI-10	22	19	22	19	86 %	40'
8'	C 310	27-VI-10	25	23	25	23	92 %	40'
7' {	C 303	25-VI-10	25	12	} 50	31	62 %	60'
{	C 309	27-VI-10	25	19				40'
5'	C 300	25-VI-10	28	8	28	8	29 %	—

TABLE XI B.

37° Centigrade.   2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
20'	C 306	25-VI-10	24	21	24	21	87 %	40'
15'	C 312	27-VI-10	25	25	25	25	100 %	40'
10' {	C 305	25-VI-10	23	9	} 48	22	46 %	—
{	C 311	27-VI-10	25	13				55'

TABLE XI C.

37° Centigrade.   6 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
25'	C 308	25-VI-10	25	25	25	25	100 %	50'
20'	C 315	27-VI-10	19	16	19	16	84 %	35'
15' {	C 307	25-VI-10	25	12	} 50	26	52 %	60'
{	C 314	27-VI-10	25	14	}			45'
10'	C 313	27-VI-10	19	6	19	6	32 %	—

TABLE XI D.

37° Centigrade.   24 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
20'	C 318	28-VI-10	25	17	—	—	68 %	60'
15'	C 317	28-VI-10	19	10	—	—	52 %	60'
10'	C 316	28-VI-10	24	8	—	—	33 %	—

TABLE XII A.

38° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
30'	C 320	7-VII-10	33	33	33	33	100 %	45'
20'	C 326	8-VII-10	30	30	30	30	100 %	40'
15'	C 338	11-VII-10	25	24	25	24	96 %	35'
10'	C 337	11-VII-10	20	16	50	35	70 %	40'
	C 319	7-VII-10	30	19				60'
8'	C 336	11-VII-10	25	13	25	13	52 %	45'
5'	C 325	7-VII-10	33	7	33	7	21 %	—

TABLE XII B.

38° Centigrade.   2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
30'	C 340	11-VII-10	25	23	—	—	92 %	40'
20'	C 328	8-VII-10	29	24	—	—	83 %	45'
15'	C 332	9-VII-10	25	15	—	—	60 %	55'
10'	C 327	8-VII-10	32	10	—	—	31 %	—
8'	C 339	11-VII-10	25	9	—	—	36 %	—
5'	C 331	9-VII-10	25	3	—	—	12 %	—

TABLE XII C.

38° Centigrade.   4 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
40′	C 330	8-VII-10	25	25	—	—	100 %	50′
30′	C 322	7-VII-10	25	16	—	—	64 %	55′
20′	C 329	8-VII-10	25	7	—	—	28 %	—
10′	C 321	7-VII-10	33	6	—	—	18 %	—

TABLE XII D.

38° Centigrade.   6 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
45′	C 335	9-VII-10	23	13	—	—	57 %	70′
40′	C 324	7-VII-10	17	10	—	—	60 %	70′
35′	C 334	9-VII-10	22	9	—	—	41 %	75′
30′	C 333	9-VII-10	25	6	—	—	24 %	—
20′	C 323	7-VII-10	17	0	—	—	0 %	—

TABLE XII E.

38°. Centigrade.   12 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
100′	C 364	9-VIII-10	16	12	—	—	75 %	100′
75′	C 363	9-VIII-10	19	14	—	—	74 %	100′
60′	C 362	9-VIII-10	17	11	—	—	65 %	95′
45′	C 361	9-VIII-10	16	6	—	—	37 %	—
30′	C 360	9-VIII-10	18	4	—	—	22 %	—

TABLE XIII A.

39° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
60′	C 349	13-VII-10	20	20	—	—	100 %	75′
40′	C 348	13-VII-10	30	25	—	—	83 %	65′
20′	C 347	13-VII-10	28	16	—	—	57 %	65′
10′	C 346	13-VII-10	25	10	—	—	40 %	70′

TABLE XIII B.

39° Centigrade.   2 hours preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
40'	C 359	15-VII-10	29	10	58	38	66 %	—
	C 352	13-VII-10	29	28				50'
20'	C 358	15-VII-10	28	4	58	23	40 %	—
	C 351	13-VII-10	30	19				55'
15'	C 357	15-VII-10	30	4	30	4	13 %	—
10'	C 356	15-VII-10	29	3	59	8	14 %	—
	C 350	13-VII-10	30	5				—

TABLE XIV A.

40° Centigrade.   1 hour preliminary warming.

Stimulation-time.	Number.	Date.	Number of plants used.	Number of plants curved.	Total number.	Total number curved.	Percent.	Reaction-time.
210'	C 298	24-VI-10	31	14	31	14	46 %	240'
180'	C 297	24-VI-10	26	13	26	13	50 %	210'
120'	C 296	24-VI-10	29	0	29	0	0 %	—
90'	C 295	24-VI-10	26	0	26	0	0 %	—
60'	C 293	22-VI-10	28	0	56	0	0 %	—
	C 294	24-VI-10	28	0				—
30'	C 19	10-III-10	50	0	50	0	0 %	—
20'	C 290	22-VI-10	20	0	20	0	0 %	—
10'	C 18	10-VI-10	50	0	75	0	0 %	—
	C 288	22-VI-10	25	0				—

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